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A system of generalizations pertaining to the organization, development and persistence, adaptation, and productivity of ecological systems and their response to toxic substances was formulated. Laboratory ecosystems composed of persistent populations of guppies, amphipods, snails and various microinvertebrates were used in examining the system of generalizations for their utility and conformity with observation. Guppy populations in the ecosystems were exploited at different rates to simulate fishing, and the systems were provided with different levels of habitat availability and energy input rates.

The laboratory communities developed different steady-state structures at different guppy exploitation rates and different levels of habitat availability and energy input. Guppies, amphipods, and snails were competitors for a common food resource, organic matter derived in part from the primary energy source, an alfalfa ration. Amphipods were also a prey of the guppies. Changes in exploitation rate and habitat availability and energy input brought about changes in the densities of all these interacting populations.

Aquarium experiments intended to evaluate the effects of dieldrin on guppy life history patterns were conducted in conjunction with the laboratory ecosystem studies. This provided the opportunity for examining some of the relationships between effects observed in experiments more like simple toxicity tests and effects observed in laboratory ecosystems. In the aquarium experiments, concentrations of dieldrin similar to those used in the laboratory ecosystems had effects on life history patterns similar to effects on life history patterns observed in the ecosystems. It is less evident how the diversity of effects on guppy populations observed in the ecosystems-- ranging from perturbation and recovery to extinction--could have been predicted from the aquarium experiments.

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# ORGANIZATION AND ADAPTATION OF AQUATIC LABORATORY ECOSYSTEMS EXPOSED TO THE PESTICIDE DIELDRIN

by

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# ABSTRACT

A system of generalizations pertaining to the organization, development and persistence, adaptation, and productivity of ecological systems and their response to toxic substances was formulated. Laboratory ecosystems composed of persistent populations of guppies amphipods, snails, and various micro-invertebrates were used in examining the system of generalizations for their utility and conformity with observational experience. The guppy populations were exploited at different rates to simulate fishing and the systems were provided with different levels of habitat availability and energy input rates.

The laboratory communities developed different steady-state structures at different guppy exploitation rates and different levels of habitat availability and energy input. Guppies, amphipods, and snails were competitors for a common food resource, organic matter derived from the primary energy energy source, an alfalfa ration. Amphipods were also a prey of the guppies. Changes in exploitation rate and habitat availability and energy input brought about changes in the densities of all of these interacting populations.

One part per billion of dieldrin was continuously introduced into four ecosystems, one at each guppy exploitation rate, at the low level of habitat availability and energy input. It was determined in ancillary experiments that 1 ppb of dieldrin probably directly affected only the guppy populations. The response of the systems to dieldrin was influenced by exploitation rate. They ranged from reduction in biomass and subsequent recovery of the unexploited guppy population to extinction of the most heavily exploited populations. Amphipod populations increased as a result of reduction in guppy biomasses.

Guppies exhibited different life history patterns at different community structures, which were generated by different rates of exploitation and levels of habitat availability and energy input. As exploitation rate increased, guppies exhibited increased size-specific growth and reproduction. These changes in life history pattern were interpreted as adaptations enabling the populations to persist at high exploitation (mortality) rates where length of life and consequently, number of reproductions per lifetime was reduced. Dieldrin altered life history pattern by reducing survival, growth, and reproduction. Thus, the toxicant may have caused extinction of the heavily exploited population by effectively preventing it from exhibiting the life history patterns that adapted the population to persist at high exploitation rates.

Aquarium experiments intended to evaluate the effects of dieldrin on guppy life history patterns were conducted in conjunction with the laboratory ecosystem studies. This provided the opportunity for examining some of the possible relationships between effects observed in experiments more like simple toxicity tests and effects observed in laboratory ecosystems. In the aquarium experiments, concentrations of dieldrin similar to those used in the laboratory ecosystems had effects on life history patterns similar to effects on life history patterns observed in the ecosystems. It is less evident how the diversity of effects on populations observed in the ecosystems -- ranging from perturbation and recovery to extinction -- could have been predicted from these individual organism experiments.

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# INTRODUCTION

The introduction to this report is an attempt to formulate a system of generalizations pertaining to the organization, development and persistence, adaptation, and productivity of ecological systems and their response to toxic substances. We believe it is the development and ultimately use of systems of generalizations like these, and not any particular empirical results or methodologies, that will be of most importance in understanding and managing toxic substances. These generalizations are derived from a conceptual framework (Warren et al., 1979) pertaining to the nature of biological systems and from ecological theory. Many, if not most, of the statements are implicit in extant ecological theory although perhaps they have not been stated and organized in just this way. The generalizations certainly do not encompass all of ecological knowledge. We view them as an attempt at achieving some sort of synthesis and thus, at this point, as a dynamic structure subject to extension, revision, and clarification.

Much of this report deals with long-term research conducted on the effects of a toxicant on the organization and adaptation of laboratory ecosystems. The laboratory ecosystems are composed of persistent populations of guppies, snails, amphipods, and various microinvertebrates. The guppy populations are exploited at different rates to simulate fishing and the systems are provided with different levels of habitat availability and energy input rates. The laboratory ecosystem research is useful for examining the system of generalizations as to their utility and conformity with observational experience.

Our conceptual and theoretical views of the nature of biological systems determines the approaches we take in understanding the effects of toxic substances on them. The performances of individual organisms, populations, and communities are in continuous change. Any performance of these organismic systems, such as structure, development, replication, and persistence, can be understood as being determined by the system's capacity and its environment at a particular time (Warren et al., 1979). The capacities of organismic systems depend on their organization, which entails incorporation of organismic subsystems whose capacities and performances are concordant with the capacities and performances of their level specific environments. Systems with a given capacity will exhibit different performances under different sets of environmental conditions. Development and evolution alter the capacities of organismic systems and thus also lead to different performances. Any organismic system can be understood to have a unique realized capacity at each developmental-evolutionary state, this realized capacity being a partial expression of the potential capacity of the system in interaction with its coextensive environmental system.

Adaptation entails the maintenance of present and probable future concordance of the capacities and performances of an organismic system with the capacities and performances of its environmental system (Warren and Liss, in press). The word concordance implies the existence of harmonious and apparently rule-governed relations between the organismic system and its environmental system. The adaptive capacities and performances of organismic systems depend upon their organization. Competition, predation, human exploitation, and toxic substances alter the organization and thus the adaptive capacities of populations and communities.

A population adapts to changes in its environment through life history adaptation and through evolutionary adaptation (Warren and Liss, in press). Individual organisms have life history capacities that enable them to developmentally alter their life history patterns in accordance with changes in their environmental systems. This is life history adaptation. But, as environmental conditions fluctuate from generation to generation, natural selection brings about a change in the kinds of individual organism life history capacities composing the population. The population thus becomes made up of life history capacities that are best adapted -- most concordant -- with the environmental system. This is evolutionary adaptation.

Human exploitation and management of an ecological resource entails the exploitation of life history and evolutionary adaptive capacity of a particular population, whereby developmental adaptation and evolutionary adaptation tend to favor its persistence in the face of exploitation and increased mortality. Not only changes in exploitation but the presence of toxic substances can alter life history patterns, bring about evolutionary changes, and so alter the adaptive capacities of populations and communities. And often now, populations must adapt to both exploitation and toxic substances as well as to other factors in their environments. Thus explanation and understanding of the adaptive capacities of individual organisms, populations, and communities becomes not only of much ecological interest but of much practical importance as well.

The levels and kinds of energy and materials available to an ecological system, patterns of climatic conditions, colonization opportunities, species interactions including predation, competition, mutualism, and the spaciotemporal distribution of primary physical habitat types are joint determinants of the organizaton of systems of populations or communities. Thus these determine whatever performances including structure and persistence populations and communities may exhibit. Too often in ecological theory and observation, these determinants have been treated separately in hypotheses intended to account for differences in the diversity of communities, as may be observed along latitudinal gradients (Pianka, 1966). In recent years, some ecologists have attempted to use two or more of these hypotheses together to account for observations onn community structure and diversity (Connell, 1975; Menge and Sutherland, 1976). For clarity, these hypotheses may be stated separately, but it is as a system of generalizations that they should be employed in explanation and understanding of community organization and any of its manifestations.

The productivity hypothesis states that total energy available to a community is the primary determinant of the diversity and abundance of organisms (Connell and Orias, 1964). The time-stability hypothesis asserts that climatic constancy and length of time for species colonization are the primary determinants of community diversity (Sanders 1969). The spacial heterogeneity hypothesis states that the structural complexity of habitat is the primary determinant of species diversity (Menge and Sutherland 1976). The competition hypothesis maintains that competition among species populations for trophic and habitat resources arrayed in space and time primarily determines community composition (MacArthur 1972, and Diamond 1975). And the predation hypothesis asserts that "key" predators allow for coexistence of some competitors and thus maintain community diversity (Paine 1966, and Connell 1975).

Booty (1976) developed a model that explicitly couples the dynamics of interactions populations with one another and with prevailing system environmental conditions. The interactions are represented with systems of isoclines on phase planes. As will become apparent throughout this report, such a graphical representation allows us to bring together life history patterns, system productivity, and population system outcomes of predation, competition, resource utilization, and the presence of toxic substances, together with the production and yield of exploited populations, aspects that have not generally been unified in ecological or toxicological theory.

In a system of populations, or in a community, abundances, and distributions of the interacting populations -- the structure of the system of populations -- is in continuous developmental and evolutionary change. Even so, systems of populations can be ideally understood as being multi-steady-state systems. The way that a system is organized determines its capacity to exhibit different steady-state structures.

For each set of environmental conditions, there exists a single steady-state point on each phase plane, each of these points being a two-dimensional projection of a single, multidimensional system, steady-state point in phase space (Figure 1). The set of these points defines the steady-state structure of the system for a given set of environmental conditions. Changing conditions in the system's environment, such as exploitation rate or rate of input of energy, brings about a change in the steady-state structure of the system.

On each phase plane, trajectories represent the changes through time in biomasses of the populations composing the system. If environmental conditions are fixed, trajectories on each phase plane will converge upon the steady-state points locating the steady-state structure of the system under those conditions (Figure 2). In natural systems,

Figure 1. Phase planes and isocline systems representing the interrelationships between populations in a system represented as $E \underset{+}{\overset{-}{\rightleftarrows}} C \underset{+}{\overset{-}{\rightleftarrows}} H \underset{+}{\overset{-}{\rightleftarrows}} P \underset{+}{\overset{-}{\rightleftarrows}} R \underset{+}{\overset{-}{\rightleftarrows}} \overset{+}{\leftarrow} I$, where C,H,P, and R comprise the system and E, exploitation rate, and I, rate of energy or plant resource input, are factors in the environment of the system. Predator biomass is plotted on the y-axis of each phase plane and prey biomass is plotted on the x-axis. On each phase plane, the descending lines identified by different rates of plant resource input, I, are prey isoclines. Each prey isocline is defined as a set of biomasses of predator and prey where the rate of change of prey biomass with time is zero. The ascending lines on each phase plane are predator isoclines. Each predator isocline is defined as a set of biomasses of predator and prey where the rate of change of predator biomass with time is zero. Each intersection of a predator and prey isocline is a steady-state point where the rate of change of both predator and prey biomass with time is zero. The positions and forms of the isoclines can be deduced from response functions representing the rates of gain and loss of each of the populations (Booty, 1976; Liss, 1977). At a particular level of I and E, a single steady-state point exists on each phase plane, the set of these points defining the steady-state biomasses of C,H,P, and R. The points that define the steady-state biomasses of C,H,P,R at Med I and 0E (circles), 30E (squares), 90E (triangles) and 150E (hexagons) are shown.

In this simple system, at each energy input rate, increased E brings about reduction in steady-state biomass of C, increases in H, reductions in P, and increases in R. Increases in I shift the steady-state relationships between predator and prey to the right on each phase plane, essentially increasing the biomasses of C,H,P, and R. After Liss and Warren (1980).

Figure 1.

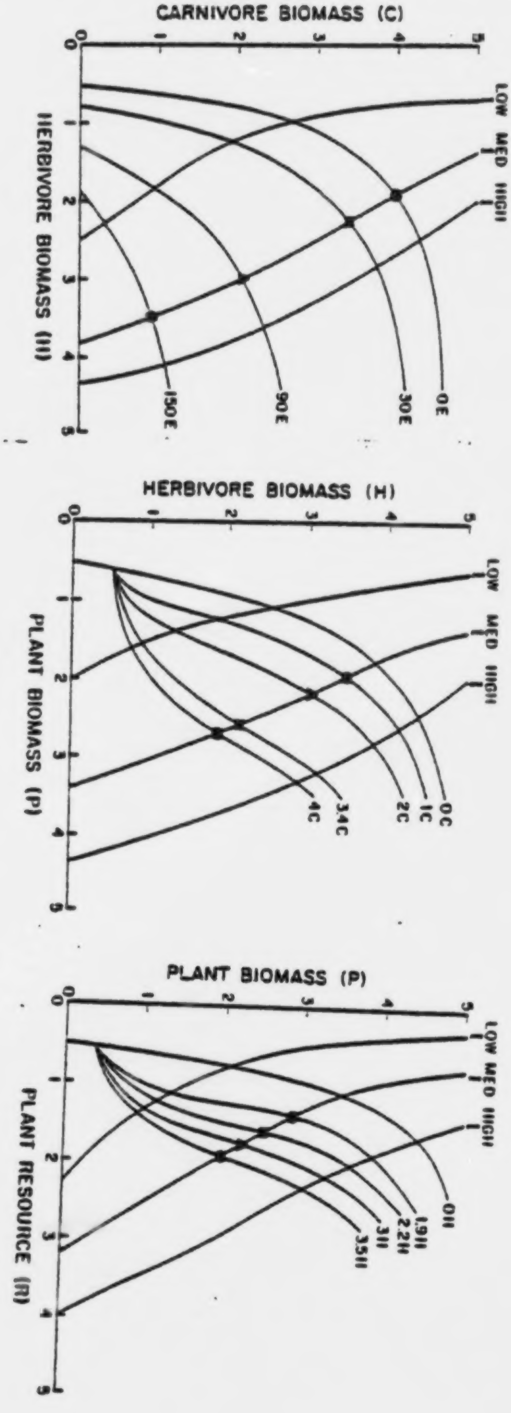
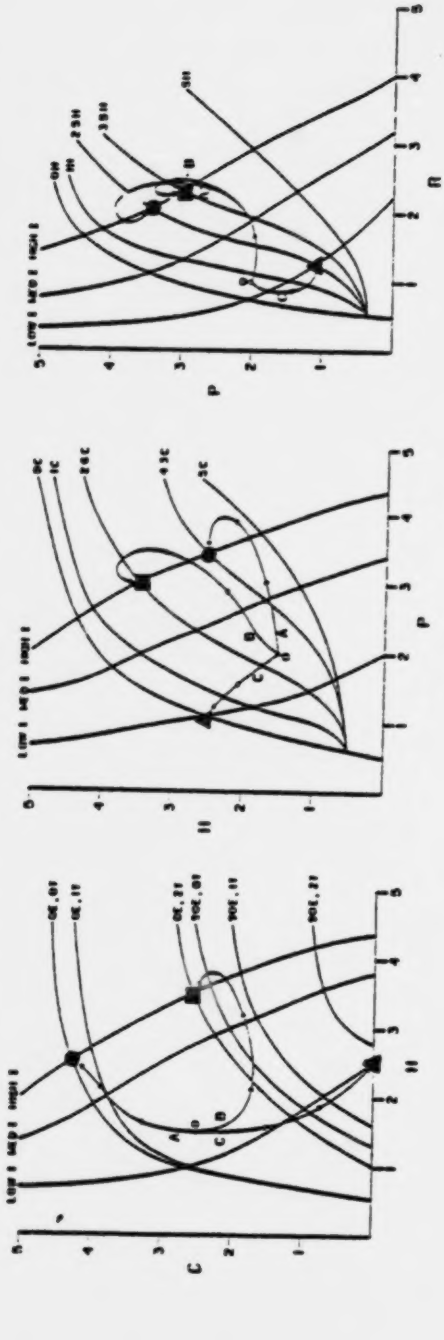

CARNIVORE BIOMASS (C)
0
1
2
3
4
5
LOW
MED
HIGH
0E
30E
90E
150E
HERBIVORE BIOMASS (H)
0C
1C
2C
3.4C
4C
PLANT BIOMASS (P)
0H
1.9H
2.2H
3H
3.5H
PLANT RESOURCE (R)

Figure 2. Phase planes and isocline systems illustrating a possible effect of different concentrations of a toxicant (T) on the structure of a simple community. In this example the toxicant directly affects only the carnivore population. Steady-state structure at 0E, 0T (circles); 0E, 2T (squares); 90E, 2T (triangles) is shown. Trajectories of biomasses of carnivore (C), herbivore (H), plant (P), and plant resource (R) converging on each of these steady-states are shown. Introduction of toxicant at a concentration of 2T reduced carnivore biomass, increased herbivore biomass, reduced plant biomass and increased plant resource at high I, 0E (compare circles and squares on all phase planes). At low I, in the absence of toxicant (0T), the carnivore is able to persist at 90E (prey isocline identified by low I intersects predator isocline identified by 90E, 0T). But, at a concentration of 2T, the carnivore population is driven to extinction at 90E (prey isocline identified by low I does not intersect predator isocline identified by 90E, 2T) At higher I, the carnivore is able to persist at 90E, 2T. Response of systems to toxicants may be affected by conditions in their environments such as rate of exploitation (mortality) of their populations or rate of energy and plant resource input. After Warren and Liss (1977).

Figure 2.



environmental conditions are rarely constant for long enough periods of time to permit systems to reach steady-states. Thus, under changing environmental conditions, systems are in continuous pursuit of an ever-shifting steady-state point.

Individual species populations form the subsystems that are incorporated into a system of populations. The position and form of isoclines on phase planes and thus the location of steady-state points in phase space is determined by the characteristics of the interacting populations. A complete set of isoclines on all phase planes provides at least a partial view of the organization of a system of populations insofar as it represents harmonious relations between the steady-state performances of interacting populations under different environmental conditions and thus at least partially represents concordance of the capacities of interacting populations. Predation, competition, mutualism, and omnivory are classes of kinds of concordant relations between the capacities of interacting populations and are determinants of the organization of systems of populations. Systems with somewhat more complex organization than that shown in Figure 1 can also be represented with systems of isoclines on phase planes.

Introduction of toxic substances can alter the structure and organization of systems of populations (Figure 2). The response of systems to toxic substances is affected by conditions in their environments such as rate of energy input and level of exploitation of their populations (Warren and Liss, 1977). In Figure 2, the carnivore population is able to persist at a low rate of energy input (low I) when it is heavily exploited (90E) if a toxic substance (T) is not present (the predator isocline identified by 90E, 0T intersects the prey isocline identified by low I). But, under these same environmental conditions at a toxicant concentration of 2T, the carnivore population is driven to extinction (C trajectory). The carnivore is able to persist, although at reduced biomass, at a toxicant concentration of 2T at low I when the carnivore is unexploited (OE), or at medium and high I when C is heavily exploited (90E). But toxicant at a concentration of 2T so altered carnivore adaptive capacity that it was no longer adapted to persist when heavily exploited at low I.

If a toxicant brings about a reduction in population density and change in system structure, the effect may be corrected by banning the toxicant and allowing the system to return to its original structure. But it is just as probable that changes in the capacity of the population or its community induced by the toxicant will make return to its original structure impossible (cf. Holling, 1973, 1978).

Individual organisms have life history capacities to exhibit different life history patterns under different sets of environmental conditions. Through such developmental alteration in the life history patterns of these individuals and through coevolutionary changes, populations and systems of populations maintain concordance with their environments. Each steady-state structure of a system of populations achieved under a given set of system environmental conditions (Figure 1) represents a particular developmental environment for individual organisms. Individuals maintain concordance with systems of populations by developing different life history patterns at different steady-state system structures (Kulbicki, 1979; Woltering, 1980). This generalization allows us to more closely couple life history patterns, populations, and systems of populations and to better understand system organization. Furthermore, through relationships of life history patterns to population density and community structure, the relevance of toxicant effects on life histories observed in simple toxicity tests to possible effects on populations and systems of populations may be better understood and their interpretation facilitated.

In a community, a single or a few populations, because of their economic or aesthetic importance, may be of special interest to society. Understanding the productivity of systems for particular populations of interest is an important practical as well as scientific goal.

The organizaton of a system of populations and levels and kinds of energy and materials available to the system determine the productivity of the system for each of its populations. Productivity was distinguished by Ivlev (1945) from production or the particular density-dependent rate of tissue elaboration for a population (Warren, 1971). Production can be calculated as the product of relative growth rate and biomass. So long as food is limiting, relative growth rate of individuals declines with increasing population biomass. A curve of production plotted against biomass is dome-shaped. Such a curve defines a level of productivity.

Steady-state carnivore production and yield curves can be derived from the relationship between steady-state carnivore and herbivore biomasses defined by the prey isoclines on the C-H phase plane, together with a relationship between carnivore relative growth rate and herbivore biomass (Booty, 1975; Liss, 1977). Changes in rate of energy input I change the productivity of the system for the carnivore population and thus alter the magnitudes of the production and yield curves (Figure 3). Furthermore, diversion of energy and material anywhere along the trophic pathways leading to a population can alter the productivity of a system

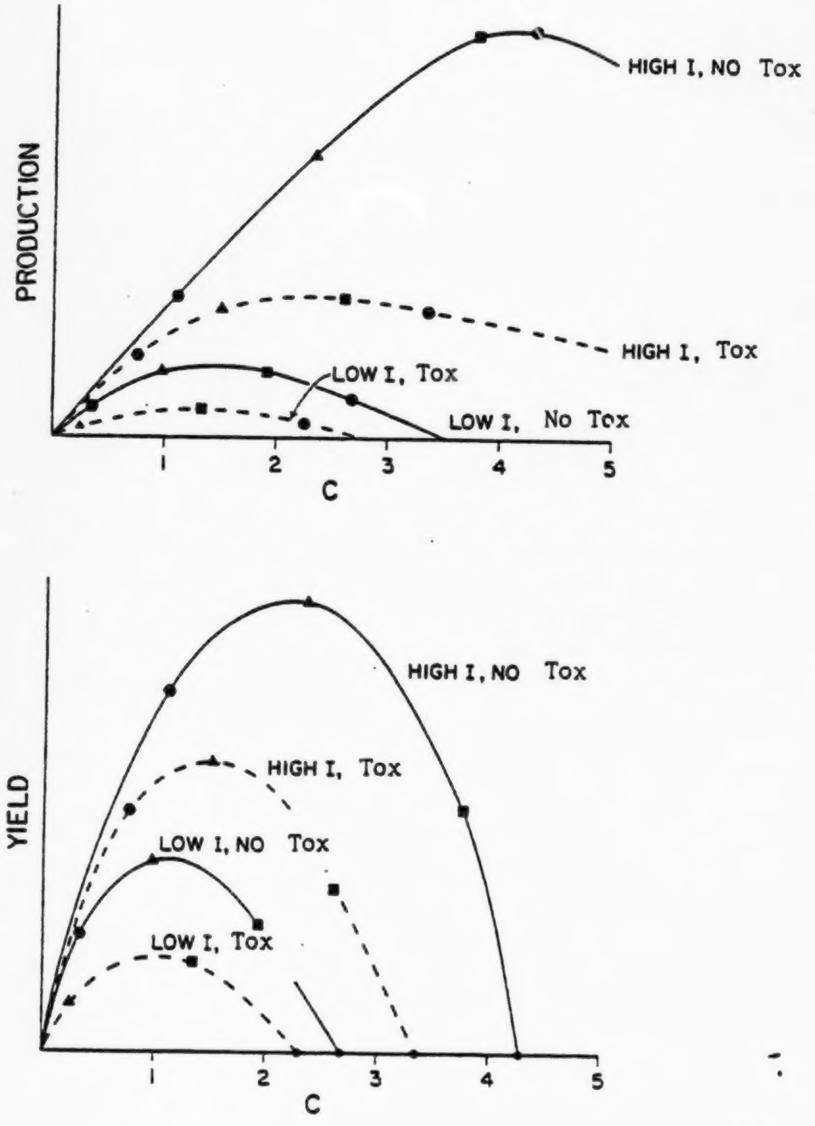


Figure 3. Impact of a toxicant T on the magnitude of carnivore steady-state production and yield curves at high and low energy input rates. Symbols indicate steady-state carnivore biomass, production, and yield at different exploitation rates ( ●-0E, ■-30E, ▲-90E, ◐150E).

for that product. This includes competition with the carnivore or competition on lower trophic levels. Production and yield, a fate of production of much importance to man, is determined not only by the life history capacities of the individuals composing the population, but also by the organization of the system. As such, production and yield are as much performances of the system as they are of the population of interest.

Toxic substances can alter productivity for a population of interest by affecting system organization or by altering the life history patterns of individuals composing the population. These kinds of alterations in productivity reduce the magnitudes of production and yield curves (Figure 3).

The goal of this research is to advance understanding of the adaptive and other capacities and performances of individual organisms, populations, and systems of populations exposed to the insecticide dieldrin. The objectives of the research include:

1. Determine and explain, under different sets of environmental conditions, the impact of dieldrin on the persistence, structure, and organization of laboratory ecosystems in terms of concordance of the capacities and performances of the incorporated populations. Environmental conditions include different levels of habitat availability and rates of input of an energy resource and different rates of exploitation of one of the populations.
2. Determine and explain the impact of dieldrin on the adaptive capacity, life history patterns, production, and yield, as well as density of the exploited population and relate these to community structure and organization and environmental conditions.
3. In separate aquarium experiment somewhat like toxicity tests, determine and explain the impact of dieldrin on maturation and age- and size specific growth and reproduction of individuals of the

exploited population and relate these results to effects on life history patterns and population density of the exploited population and on system structure and organization observed in the laboratory communities.

## CONCLUSIONS AND RECOMMENDATIONS

1. The systems of generalizations presented in the Introduction at least broadly conforms with observational experience derived from laboratory ecosystems. Ecological systems can be thought of as multisteady-state systems with steady-state structure being determined by the system's potential capacity and conditions in the system's developmental environment. Laboratory communities composed of persistent populations of guppies, snails, amphipods, and various kinds of microinvertebrates established near steady- states. Conditions in the environments of the communities such as rate of exploitation of their populations, level of habitat availability and energy input, and exposure to the insecticide dieldrin in part determined the steady-state structure that the systems developed.

2. The capacities of ecological systems depend upon the way they are organized. Trophic organization of communities entails interactions between populations such as competition, predation, mutualism, and commensalism. Population interactions can be represented on phase planes. In the laboratory ecosystems, populations of guppies, snails, and amphipods competed for a common food resource, the organic sediment. Amphipods were also prey of guppies. As a consequence of this organization, increases in exploitation rate resulted in reductions in near steady-state guppy biomass and increases in the near steady-state biomasses of their snail competitor and amphipod competitor/prey. Increases in habitat availability and energy input increased the biomasses of guppies, amphipods, and snails at each exploitation rate.

3. One ppb of dieldrin continuously introduced into the laboratory ecosystems at the low level of habitat availability and energy input directly affected only the exploited guppy populations. Other populations in the systems were affected only indirectly as a result of changes in guppy biomass. The response of the systems to dieldrin was affected by environmental conditions including rate of exploitation of the guppy population and level of habitat availability and energy input. Response to dieldrin ranged from reduction of biomass and subsequent recovery of the unexploited guppy population to extinction of the heavily exploited guppy population. It was suggested that the heavily exploited population driven to extinction at the low level of habitat availability and energy input would have been able to persist at a higher level of habitat and energy input. This is currently being evaluated experimentally. Amphipods, a competitor and prey of guppies, increased in biomass as a result of toxicant induced reduction of guppy biomass. Indirect effects on snails were unable to be determined since monitoring of snail density began after introduction of dieldrin.

4. Different near steady-state community structures were generated by different rates of exploitation and levels of habitat availability and energy input. Guppies developed different near steady-state life history patterns at different exploitation rates and levels of habitat and energy input. Thus, there was a correspondence between guppy life history pattern and community structure. At each level of habitat availability and energy input rate, increased exploitation rate reduced guppy population density and induced the following changes in life history pattern: reduced lifespan, reduced number of clutches per

life-time, increased size-specific growth, increased size at first reproduction, increased fecundity. Increases in size-specific growth and reproduction of individuals can be interpreted as life history adaptations enabling the population to persist at high levels of exploitation (or mortality), where longevity and clutch number are reduced. Guppy production and yield bear dome-shaped relationships to population biomass. Increases in habitat availability increase the magnitude of these curves.

5. Dieldrin altered guppy life history patterns by reducing survival and size-specific growth and fecundity. These alterations in guppy life history patterns resulted in reductions in the magnitude of guppy production and yield curves. At the 40 percent exploitation rate, dieldrin may have caused population extinction by effectively preventing the individuals from exhibiting life history patterns -- more rapid growth, higher fecundity, increased offspring survival -- that adapt the population to persist at high exploitation rates. Such heavily exploited populations, where rapid growth, high fecundity, and good juvenile survival are essential for persistence, may be more "sensitive" to reductions in growth, fecundity, and survival caused by toxicants than populations exploited at lower rates. The density of the unexploited guppy population was reduced by exposure to dieldrin but recovered to pre-dieldrin levels while toxicant was still being introduced. This population was apparently able to adapt evolutionarily to the pesticide, with natural selection favoring individuals with more "resistant" life histories. The "recovered" population may have been composed of individuals with quite different life history capacities than the population prior to dieldrin introduction.
6. Separate aquarium experiments more like simple toxicity tests were conducted to evaluate the effects of dieldrin on guppy life history patterns

at different food rations. Dieldrin concentrations in these experiments were similar to the concentration to which the laboratory ecosystems were exposed. Guppy life history patterns observed at different food rations were broadly similar to near steady-state life history patterns observed at different exploitation rates and community structures in the laboratory ecosystems. Thus, different food rations in aquarium experiments generated life history patterns similar to those occurring at different exploitation rates. Perhaps life history patterns observed in these simple experiments can be thought of, in the broadest sense, as steady-state life history patterns that would exist at some steady-state community structure generated by some fixed set of environmental conditions. Thus, using ecological theory, perhaps meaning can be "written onto" the results of such simple experiments. Effects of dieldrin on life history patterns observed in aquarium experiments resembled effects observed in the laboratory ecosystesm -- reduced juvenile survival and decreased size-specific growth and reproduction. However, it is not as evident how the diversity of effects on population abundance, ranging from perturbation and recovery at zero percent exploitation to extinction at 40 percent exploitation, could have been predicted from these simple aquarium experiments. Perhaps, with appropriate theory, such effects would have become apparent. Interpretation of simple aquarium experiments is not a matter of direct extrapolation to complex systems. Ecological theory should be used as a "vehicle" of extrapolation, and it is in the context of such theory that results of simple aquarium experiments can be given meaning.

# MATERIALS AND METHODS

## *Laboratory Ecosystem Experiments*

### Biological and Physical System

Sixteen aquatic ecosystems were established at the Oak Creek Laboratory of Biology. Each was a multispecies system composed of persistent populations of guppies (*Poecilia reticulata*), amphipods (*Gammarus fasciatus*), snails (family *Planorbidae*), planaria (*Dugesia sp.*), and benthic microinvertebrates including flagellates, rotifers, nematodes, gastrotrichs, and protozoans. Green and blue-green algae and diatoms were present. In addition, each laboratory system had fifty grams of the aquatic plant *Ceratophyllum demersum* maintained as cover for the newborns of the cannibalistic adult guppies. Habitat and escape cover for invertebrates were provided by a substrate of 1.5 cm quartzite gravel four centimeters deep. A gelatinous mixture of 60 percent alfalfa and 40 percent Oregon Test Diet (Sinnhuber et al. 1977) served as the primary energy input in the laboratory ecosystem.

Each laboratory system was maintained in a fiberglass tank measuring 1.2m x 1.1m x 0.4m and holding 560 liters of water. This was continuously exchanged by a 600 milliliter per minute flow of heated well water. Water temperature (21 ± 1°C), dissolved oxygen (8.2 ± 0.5 ppm), and pH (7.8 ± 0.1) were maintained at nearly constant levels. Fluorescent lights above each tank provided an average intensity of about 20 footcandles at the water surface. Photoperiod was controlled by a timer set for 14 hours light and 10 hours darkness.

## Experimental Design (Phase I)

Initially all 16 laboratory ecosystems had a similar experimental design (identified as low energy input and low habitat availability) in which there were three circular nests of gravel covering 20 percent of the bottom area of each tank, and a 0.6 gram per tank daily alfalfa ration was provided. In April 1975, 200 amphipods were stocked in each system. Sediment accumulation and development of a benthic microflora and microfauna ensued. Snails were introduced with the aquatic plants and persisted at low densities.

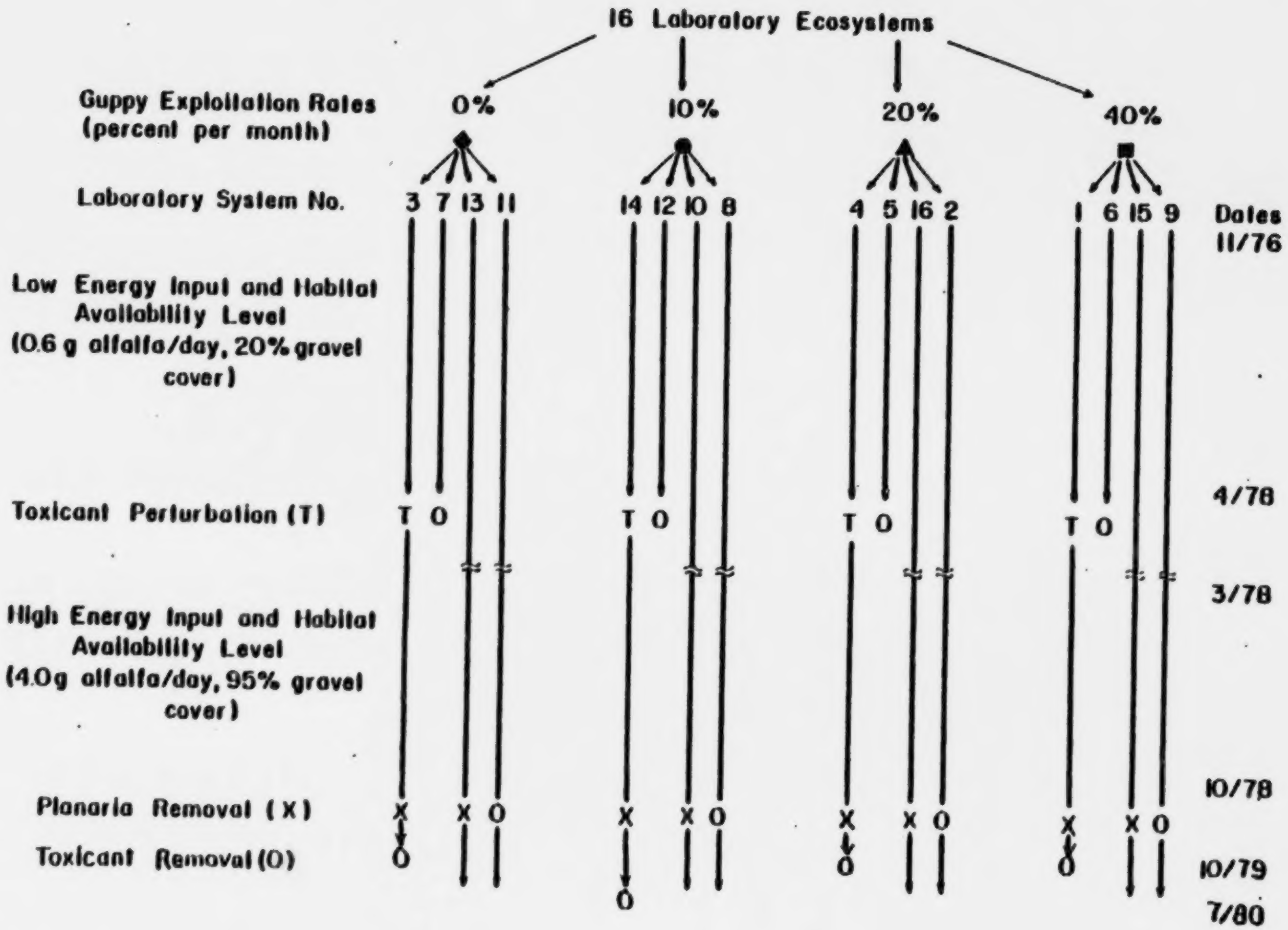
By November 1976, guppies were stocked into all systems and a monthly sampling program was initiated. Monthly exploitation rates for the guppies were set at 0, 10, 20, or 40 percent of the poulation biomass, four systems being exploited at each level (Table 1).

## Experimental Design (Phase II)

In March 1978, eight of the laboratory ecosystems (two at each guppy exploitation level) were modified to establish a higher level of energy input and habitat availability. The gravel habitat and escape cover was increased to cover 95 percent of each tank bottom. Energy input was increased to 4.0 grams of alfalfa ration daily. The monthly sampling procedure was continued unchanged.

In April 1978, the organochlorine insecticide dieldrin was introduced so as to maintain a concentration of 1 part per billion (ppb) in four of the low energy and habitat systems (one at each guppy exploitation level).

Table 1. Experimental design and chronological order of experimental manipulations. Sixteen laboratory ecosystems were established in April 1975 at the low level of habitat availability and energy input rate. Guppies were introduced and a 28-day sampling-exploitation schedule was begun in November 1976. Four systems were continuously exposed to 1 ppb dieldrin in April 1978. At the same time, eight systems were shifted to the high level of habitat availability and energy input. Dieldrin introduction into the four systems at low habitat and energy input was terminated in September 1979.


16 Laboratory Ecosystems
Guppy Exploitation Rates (percent per month)
0%
10%
20%
40%
Laboratory System No.
3 7 13 11
14 12 10 8
4 5 16 2
1 6 15 9
Dates
11/76
Low Energy Input and Habitat Availability Level (0.6 g alfalfa/day, 20% gravel cover)
Toxicant Perturbation (T)
T O
T O
T O
T O
4/78
3/78
High Energy Input and Habitat Availability Level (4.0g alfalfa/day, 95% gravel cover)
10/78
Planaria Removal (X)
X X O
X X O
X X O
X X O
Toxicant Removal (O)
O
O
O
O
10/79
7/80

## Sampling Procedures

Organisms in each laboratory ecosystem were censused and its guppy population exploited every 28 days. Extreme care was taken to perturb the systems as little as possible during sample. Guppies were netted from the tanks. Individual length and weight measurements were taken for immature guppies (standard length of 10 to 14 millimeters) and for mature females (standard length greater than 14 millimeters). Total number and weight were recorded for mature males and for newborns (standard length less than 10 millimeters).

The method of exploitation was similar to that employed by Liss (1974). A systematic exploitation schedule was developed for each exploitation rate. The schedule provided for the removal of a proportion of the population corresponding to the exploitation rate. At each exploitation rate, all sizes of fish were exploited with the same intensity.

Total population and size-class biomasses (i.e. the combined weight of individuals) and yields (i.e., the weight of the catch at a given sampling date) were calculated for each guppy population. Total population and size-class production (i.e., the amount of tissue elaborated by the population or size-class between sampling dates) were estimated using the difference between the initial and final biomasses of the population and size-class over the 28-day intervals (Chapman 1968). Final biomasses were adjusted for any known mortalities and for fish changing size classes over the interval. Production includes somatic and reproductive (eggs and embryos) tissue elaboration. Density and size composition of the population, growth and survival of individuals, and fecundity of exploited females were also determined and related to environmental factors and to exploitation.

The gravel substrate, contained by wire screen, and the Ceratophyllum were removed from the tanks and rinsed to dislodge invertebrates. Amphipods, snails, planaria, and sediments plus associated micororganisms were then removed by a siphon and a net. Individuals in each macroinvertebrate population were sized, counted, and then weighed as a group. The Ceratophyllum was weighed and restocked as necessary to maintain 50 grams in each system. Three one-percent subsamples of the sediment from each system were obtained with a sample splitting device. Dry weight and organic matter content were determined. The samples were dried at 70°C for 72 hours and then ashed for three hours at 500°C. Organic nitrogen content was determined by standard microkjeldahl technique (Berg and Gardner, 1978). Microorganisms were identified and their densities estimated with the aid of a Sedgwich Rafter Cell (APHA 1971). All amphipods, snails, remaining sediments with microorganisms, and unexploited fish were returned to the tanks.

The insecticide dilution and delivery system was similar to the continuous flow dilution apparatus described by Chadwick et al. (1972). A solution having a constant toxicant concentration was produced by passing water through a column of 1.5 cm quartzite gravel coated with technical grade dieldrin. Concentrations of dieldrin were determined weekly in laboratory ecosystem water samples and periodically in tissue samples of guppies, snails, plants, and sediments. Following standard extraction procedures, analysis was done using a Varian-areograph 2000 gas chromatograph equipped with an electron capture detector.

## Methods Used to Determine Effects of Dieldrin on Guppy Life History Patterns Determined in Separate Aquarium Experiments

Aquarium experiments were conducted to evaluate the effects of dieldrin on guppy life history patterns. These experiments were similar to many kinds of toxicity tests on individual organisms. The purpose of these experiments was to gain some understanding of the relationship of effects observed on life history patterns in relatively simple tests to effects on life history patterns, populations, and communities in the more complex laboratory ecosystems. Some insight into the relevance of such simple tests in understanding and predicting effects in more complex systems may thus be obtained.

Seven hundred newborn guppies (approximately 5 mm in length) were collected over a period of one week and divided into two groups of 350 fish each. Fish were fed live tubificid worms (Tubifex sp.). Each group received a different food ration. Food ration levels for individuals in each group represent a fixed proportion of the maximum daily food consumption rate per individual. The high ration (HR) represents 0.66 of the maximum daily food consumption rate and the low food ration (LR) represents 0.33 of the maximum daily food consumption rate. Since maximum daily food consumption rate is dependent upon body weight, all food rations are expressed as a decimal fraction of body weight:

1) $f_1 = 0.33\ M$ for the low ration and

2) $f_2 = 0.66\ M$ for the high ration

$f_i$ = daily food ration per individual as a proportion of body weight

M = maximum daily food consumption rate per individual as a proportion of body weight

In fish, maximum daily food consumption rate, as a fraction of body weight, declines as body weight increases. Preliminary experiments were conducted to determine the maximum daily consumption rate per individual for different size classes of both male and female guppies (Kulbicki, 1980). From the results, daily food rations, as a fraction of body weight, were determined from equations 1 and 2. Total daily food ration per individual is given by:

3) $F_i = f_i W$

where W is body weight. As the fish grew, their ration was adjusted in accordance with changes in their maximum daily food consumption rate and body weight. All fish were weighed weekly and their food rations were adjusted accordingly. Fish were fed once a day.

Both groups of newborn guppies were held in control water and fed control food, at the appropriate ration levels, until sexual maturity was reached. Mature males were identified by the presence of a gonopodium. Fish 16 mm and over without a gonopodium were considered to be females. When sexual maturity was reached, 30 females from each group were selected. Each of these females was placed in a seven liter aquarium. At each ration level, ten females received control food and control water, ten females were continuously exposed to 1 ppb of dieldrin in the water and 2 ppm of dieldrin in the food (low dieldrin or LD), and ten females were exposed to two ppb in the water and four ppm in their food (high dieldrin or HD). The experimental design is shown in Table 2. A pesticide dilution system similar in design and principle to the continuous flow dilution apparatus described by Chadwick et al. (1973) was used to introduce the appropriate concentrations of dieldrin into the experimental chambers. Dieldrin concentrations 2 and 4 ppm in the food were obtained by holding the tubificid

Table 2. Experimental design showing the number of juvenile, adult female, and F-1 generation juveniles at each treatment. All F-1 generation fish were from the second clutch of parental females.

| | | High Ration | | | Low Ration | |
|---|---|---|---|---|---|---|
| | Control | Low Dieldrin | High Dieldrin | Control | Low Dieldrin | High Dieldrin |
| Parental Fish | | | | | | |
| Juveniles | 350 | 0 | 0 | 350 | 0 | 0 |
| Adult Females | 10 | 10 | 10 | 10 | 10 | 10 |
| F-1 Generation | | | | | | |
| Juveniles | 5 Clutches | 5 Clutches | 5 Clutches | 5 Clutches | 5 Clutches | 5 Clutches |

worms for 24 hours in flowing water containing, respectively, 5 ppb and 10 ppb of dieldrin.

One male was put with each female for a period of 24 hours each week to ensure fertilization. Since guppies are cannibilistic on their young, plants (Ceratophylum demersum) were placed in each tank to provide cover for the newborn. Newborn fish were collected every morning (birth almost always occurs at night), and their number and weight were recorded along with the age and weight of the mother. Age- and size-specific growth, age and size at first reproduction, and age- and size-specific production of offspring of parental were determined from birth through four reproductions.

Newborn fish from the second clutch produced by each of five females from each treatment were raised as the F-1 generation. Each of these groups of newborn fish were raised at the same food ration and dieldrin concentration as their parents. Juvenile survival and growth, sex ratio at maturity, and body composition were recorded.

The intrinsic rate of increase, r, is a convenient parameter for summarizing the possible population effects of changes in individual survival and fecundity and was determined for parental fish at each treatment. Lotka (1925) showed that if the age schedules of survival ($l_x$) and reproduction ($m_x$) remain constant, a population will develop a stable age distribution and population number, N, will change according to the equation:

$$dN/dt = rN$$

where r is the intrinsic rate of increase. The age schedule of survival and reproduction will remain constant only if environmental conditions remain constant and birth and death rates are not affected by changes in population density. Furthermore, as Birch (1948) illustrated in his examination of the effects of temperature and moisture on the intrinsic rate of increase of grain beetles, a particular value of r exists for each particular set of environmental conditions. Thus, r has meaning only in the context of the environmental conditions under which it was determined. In natural systems, environmental conditions are continuously changing, and birth and death rates are density-dependent, making direct applicability of laboratory determinations of r to natural systems tenuous. The concept of intrinsic rate of increase directs our attention to life history characteristics of the individual that may be important in population growth, and provides a means of evaluating how population growth and persistence could be affected by changes in life history characteristics of the individual induced by changes in environmental conditions or the presence of toxic substances.

The calculation of r was based upon the arithmetic approximation given by Birch (1948) for:

$$\sum_{x=0}^{x=} l_x m_x e^{-rx} = 1$$

Given the $l_x$ and $m_x$ schedule, the intrinsic rate of increase r was found by substituting trial values of r in the equation until the equation had a value of approximately one.

## RESULTS AND INTERPRETATION

### Trophic Organization of the Laboratory Ecosystems

Trophic organization entails that aspect of community organization based on interactions between species populations for food resources. Other aspects of community organization include life history and habitat organization. Figure 4 represents the inferred trophic interrelations in the laboratory ecosystems. This synthesized view can be taken to be an organismic system and environmental system which together form an ecological system in space and time.

### Organismic System

The organismic system is a system of populations that includes predator, prey, and competitor populations. Organic sediments including the alfalfa ration and microorganisms were the common prey for the three major populations: guppies, amphipods, and snails. Copepods were inadvertently introduced with amphipods but died out early in the study. Alfalfa ration, feces, decomposed plants and animals, and benthic microorganisms made up the 60 to 80 percent of sediments that were organic. The mean organic nitrogen content of the sediments was $3.0 \pm 0.5$ percent for the 16 systems over 34 months. The microorganism component included nematodes, flagellates, rotifers, gastrotrichs, and protozoans (Finger, 1980). An apparent link between this benthic subsystem and the major predators was a protozoan - nematode - guppy trophic chain. Alfalfa input, 0.6 or 4.0 grams per day, was the major source of sediment differences between tanks at low and high energy input levels.

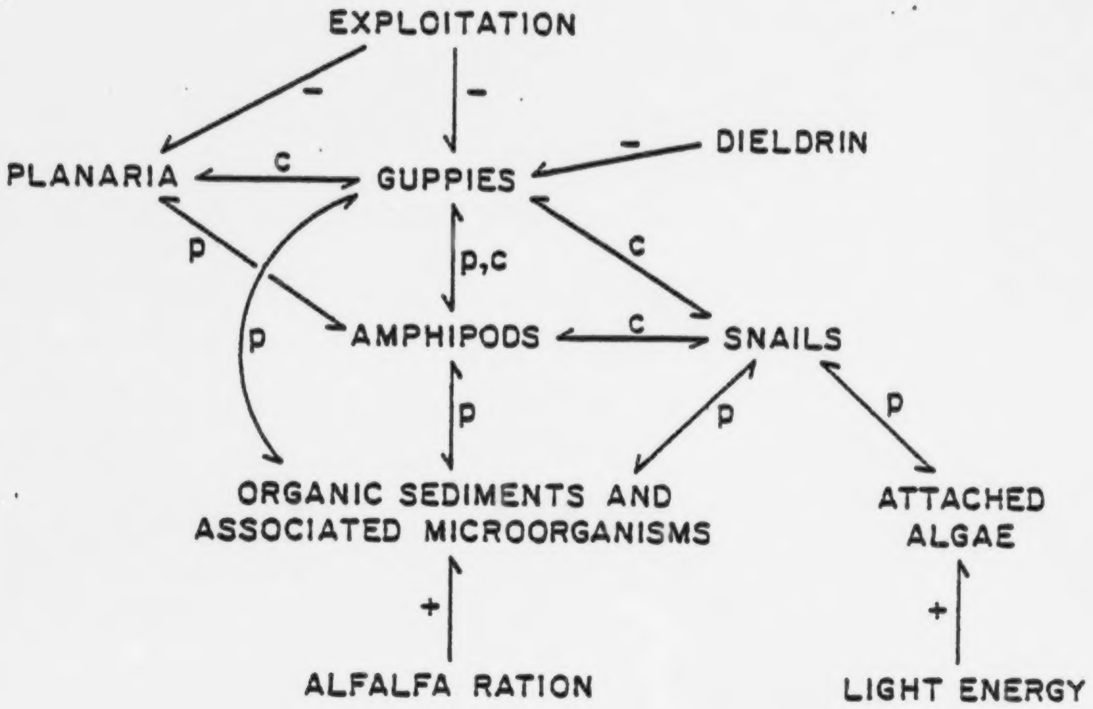

EXPLOITATION
-
-
PLANARIA
c
GUPPIES
-
DIELDRIN
p
p,c
c
p
AMPHIPODS
c
SNAILS
p
p
p
ORGANIC SEDIMENTS AND
ASSOCIATED MICROORGANISMS
ATTACHED
ALGAE
+
+
ALFALFA RATION
LIGHT ENERGY

Figure 4. Kinetic diagram representing inferred trophic interrelations in the laboratory ecosystems. Population interactions are designated as predation (p) or competition (c). Exploitation, dieldrin, alfalfa ration, and light energy are variable environmental factors.

Guppies are omnivorous, live-bearing, cannibalistic fish. Adult females (up to 42 mm and 2.0 grams) and mature males (up to 20 mm and 0.1 grams) were observed consuming the alfalfa ration, sediments, and amphipods. Stomach samples showed the presence of materials and microorganisms identified in the sediments, plus amphipod parts. Newborn guppies were observed eating alfalfa and picking through the sediments.

The amphipods in these laboratory systems were herbivorous crustaceans that ranged in size from 0.5 to 15.0 millimeters ($4 \times 10^{-5}$ to $4 \times 10^{-3}$ grams). They were observed feeding in the sediments and on the alfalfa ration. Amphipods moved freely throughout the tank and were found among the rocks, on the plants, and on the sides of the tanks when guppies were absent or at low densities. Their movement was usually limited to among the rocks and the sediment when guppies were present. Amphipods were prey of the guppy populations as well as competitors for the alfalfa ration.

Later in the experiment, planaria were inadvertently introduced and were more effective predators on amphipods than were guppies, the amphipods being unable to escape from planaria in the rock substrate habitat. Planaria were observed in all systems at low densities (i.e., 1 to 30 individuals) as early as October 1977. Following the increase in alfalfa input and substrate cover in eight systems, amphipod populations increased up to 15 times in biomass. Planaria populations increased following the increase in amphipods, and this led to drastic declines in amphipod populations. Complete elimination of planaria by exploiting them in four high productivity systems allowed the amphipods to again increase. Planaria were not exploited in the remaining four systems at high productivity and they eventually eliminated all the amphipods.

Snails were introduced as eggs attached to the aquatic plant Ceratophyllum. Snails were observed eating attached algae on the sides and bottom of the tanks as well as feeding in the sediments. They were competitors of both guppy and snail populations for the alfalfa ration. High alfalfa input brought about dramatic increases in snail biomasses. Censusing of snail populations in both high and low productivity systems was initiated about this time. Losses of snails to parasitism, predation on eggs, and other mortality was unaccounted for in these systems.

Attached algae included a mixture of blue-green and green algae and diatoms. These algae and associated microorganisms were a food resource for snails and other species in the laboratory systems. Algal density varied between tanks from essentially macroscopically non-visable levels to a solid green-brown mat. Differences in algal density and sediment accumulation patterns had apparent effects on resulting structure and organization of the systems. More detailed evaluation of the structure of the algal system and its role in the community is presently being undertaken.

## Environmental System

The manipulated environmental components of the laboratory ecosystems included habitat availability, energy and material input, guppy removal by exploitation, and introduction of the toxicant dieldrin. Alfalfa was the major energy source, as was made apparent by increases in population biomasses corresponding to the change from 0.6 to 4.0 grams per day of alfalfa ration. The organic nitrogen content of the alfalfa ration was 3.0 percent. Light levels were kept relatively low to prevent blue-green algae blooms. Intensities ranged from 15 to 23 foot-candles at the surface of the water and were directly correlated to location of the tanks in the laboratory.

Monthly exploitation of the guppy populations simulated the impact of fishing. Heavy exploitation resulted in size distributions occasionally having up to 80 percent of a population's biomass residing in one large female. More or less than the intended percentage of biomass was thus often exploited in any one month. This led to some fluctuations in population biomass; over many months, however, mean exploitation rates were near the intended percentages.

The environmentally stable insecticide dieldrin was introduced at a concentration of 1 ppb to evaluate the response of the laboratory ecosystems to toxicant at different rates of input and exploitation. Means and standard deviations of dieldrin concentrations in weekly water samples were: system No. 1, 0.95 ± 0.09 ppb; system No. 3, 0.98 ± 0.08 ppb; and systems No. 4 and 14, 0.96 ± 0.08 ppb dieldrin.

Through food and water, the lipophilic dieldrin accumulated in tissues of the organisms and in the sediments. To obtain enough tissue to perform analysis, juvenile, male, and smaller female guppies had to be combined into a single sample. The mean tissue concentration of such combined samples was 11.2 ppm. Very large females (28 mm to 38 mm in length) provided enough tissue to be analyzed individually. Tissue concentrations of these fish ranged from 29.0 to 45.0 ppm. These high tissue concentrations probably result in part from accumulation of dieldrin in eggs and developing embryos being carried by the females. The mean concentration of dieldrin in the tissues of snails (including shells) was 0.87 ppm and the concentration in sediments was 7.5 ppm.

In nature, populations persist through interactions and adaptations in complex and fluctuating environments. Figure 4 begins to account for some of the major trophic interactions including predation, competition, and omnivery in the laboratory systems. These interactions along with prevailing environmental conditions resulted in changes in community structure. The pattern of organization inferred for the laboratory systems will be used to explain observed dynamic and near steady-state community structure.

## Dynamic and Near Steady-State Structure of the Laboratory Ecosystems

Co-occurring biomasses of two interacting populations can be plotted on coordinate axes forming a phase plane. This graphical procedure explicitly couples the dynamics of interacting populations to one another. Dynamic structure is represented by the trajectories connecting the points. Under constant environmental conditions, the trajectory of coordinate biomasses may track toward a steady-state point on the phase plane; changing environmental conditions alter the direction of the trajectory toward another steady state. Near steady-state structure for the laboratory systems for each set of environmental conditions was assumed when populations fluctuated in a very restricted area of phase space relative to previous and succeeding fluctuations.

A phase plane representation of near steady-state relative to non-steady-state behavior of guppy and amphipod populations for four of the laboratory systems, one at each level of guppy exploitation, at low energy input and at high energy input, is shown in Figure 5. Guppy and amphipod populations achieved near steady states at low energy input, with near steady-state biomasses being determined by guppy exploitation rate as well as energy input rate. Increased energy input rate resulted in establishment of new near steady-states. At each exploitation rate, the near

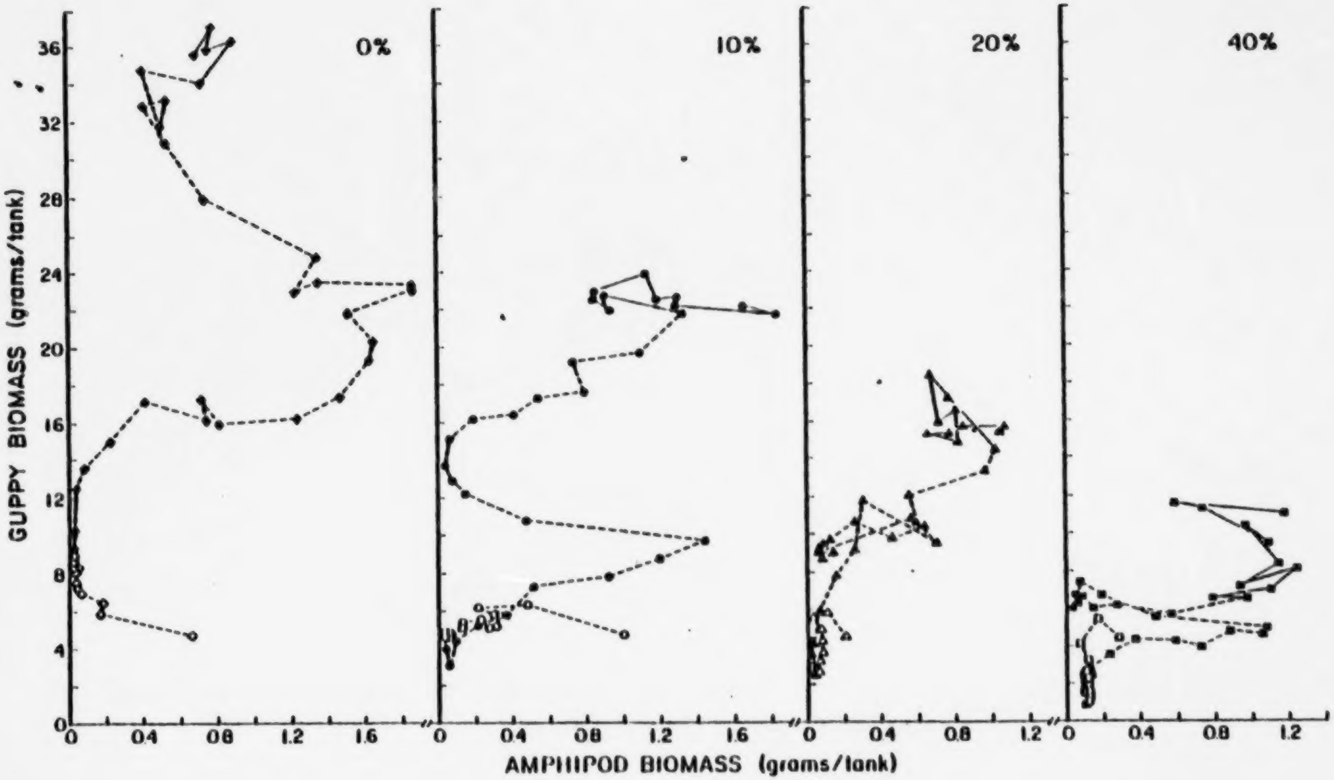


Figure 5. Guppy-amphipod phase planes showing near steady-state and nonsteady-state behavior at four guppy exploitation rates at high and low levels of habitat availability and energy input rate. Open symbols designate behavior at low, and solid symbols behavior at high habitat and energy input. Dashed trajectories designate nonsteady-state behavior and solid trajectories are taken to be near steady-state behavior.

steady-state biomasses of both populations were greater at the high rate of energy input than at the low rate. These and other results make it apparent that the laboratory communities were multi-steady state systems, (See also Figure 1). We take the steady-state system structure to be determined by system capacity and conditions in the system's environment.

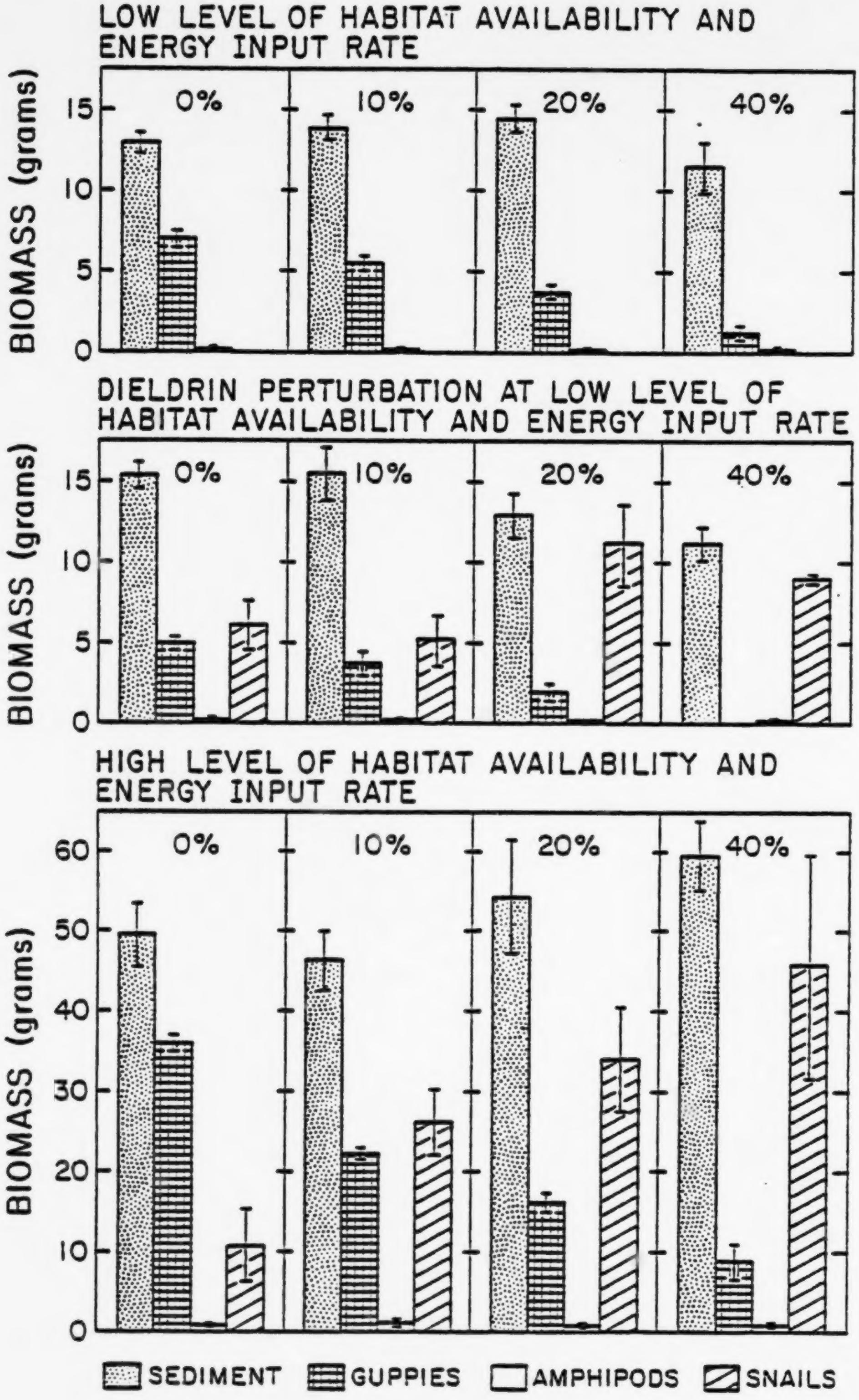
The effect of energy input rate, exploitation rate, and dieldrin on the near steady-state structure of the laboratory ecosystems is shown in Figure 6. Structure is represented as the mean biomasses of the populations when they were near steady-states. Guppies and snails were the dominant organisms in the communities. Amphipods were also present but at much lower densities. Also present in the communities but not represented in Figure 6 is the microorganism component composed of populations of euglenoid flagellates, protozoans, ciliates, amoebas, nematodes, rotifers, and gastrotrichs.

Changes in exploitation rate, habitat availability, and energy input rate, and exposure to dieldrin brought about changes in community structure and organizaton. At each level of habitat and energy input, increased exploitation rate reduced guppy biomass and increased the biomass of amphipods and snails. At the low level of habitat availability and energy input, organic sediment densities appeared to be little affected by changes in exploitation rate.

Increased habitat availability and energy input rate brought about increases in the biomasses of all populations and, thus, in total community biomass. The systems shown in Figure 6 are those from which planaria were removed. In the systems in which planaria were not removed, amphipods, one of their principal prey, became extinct. These systems have not yet established near steady-states.

Figure 6. Histograms showing steady-state biomasses of guppies, snails, amphipods, and organic sediment at the low level of habitat availability and energy input rate prior to and after introduction of dieldrin and at the high level of habitat availability and energy input.

Figure 6.


LOW LEVEL OF HABITAT AVAILABILITY AND ENERGY INPUT RATE
DIELDRIN PERTURBATION AT LOW LEVEL OF HABITAT AVAILABILITY AND ENERGY INPUT RATE
HIGH LEVEL OF HABITAT AVAILABILITY AND ENERGY INPUT RATE
BIOMASS (grams)
0
5
10
15
20
30
40
50
60
0%
10%
20%
40%
SEDIMENT
GUPPIES
AMPHIPODS
SNAILS

At the low level of habitat availability and energy input, protozoans, nematodes, and rotifers were the predominant microinvertebrates. Ciliates and euglenoid flagellates were present at low densities. At the high level of habitat availability and energy input, amoebas, nematodes, rotifers, and gastrotrichs occur infrequently in these systems.

Exposure to dieldrin altered community structure, but not to the same degree as did changes in habitat and energy input. The predominant effect was reduction in guppy biomass, with the guppy population exploited at 40 percent being driven to extinction.

Phase planes and isocline systems will be used to explicate the organization of these systems, including species interactions such as predation, competition, and omnivery, to account for and so explain changes in the structure of the laboratory ecosystems.

## Predation, Competition, and System Organization at Different Levels of Habitat Availability, Energy Input Rates, and Exploitation Rates

Near steady-state system structure was determined by the interactions between the population composing the system and conditions in the system's environment. At each level of habitat availability and energy input rate, changes in rate of exploitation of the guppy populations influenced near steady-state system structure by affecting not only guppy biomass but the biomasses of the guppies' prey and competitors as well.

At the low level of habitat availability and energy input, increased exploitation rate brought about reductions in near steady-state guppy biomass and increases in near steady-state amphipod and snail biomasses. As exploitation rate was increased from zero to forty percent, near steady-state guppy biomass decreased from approximately 9.0 to 1.0 grams (Figure 7). Apparently because of reduction in intensity of predation and competition, near steady-state biomasses of amphipods tended to increase as guppy biomass declined.

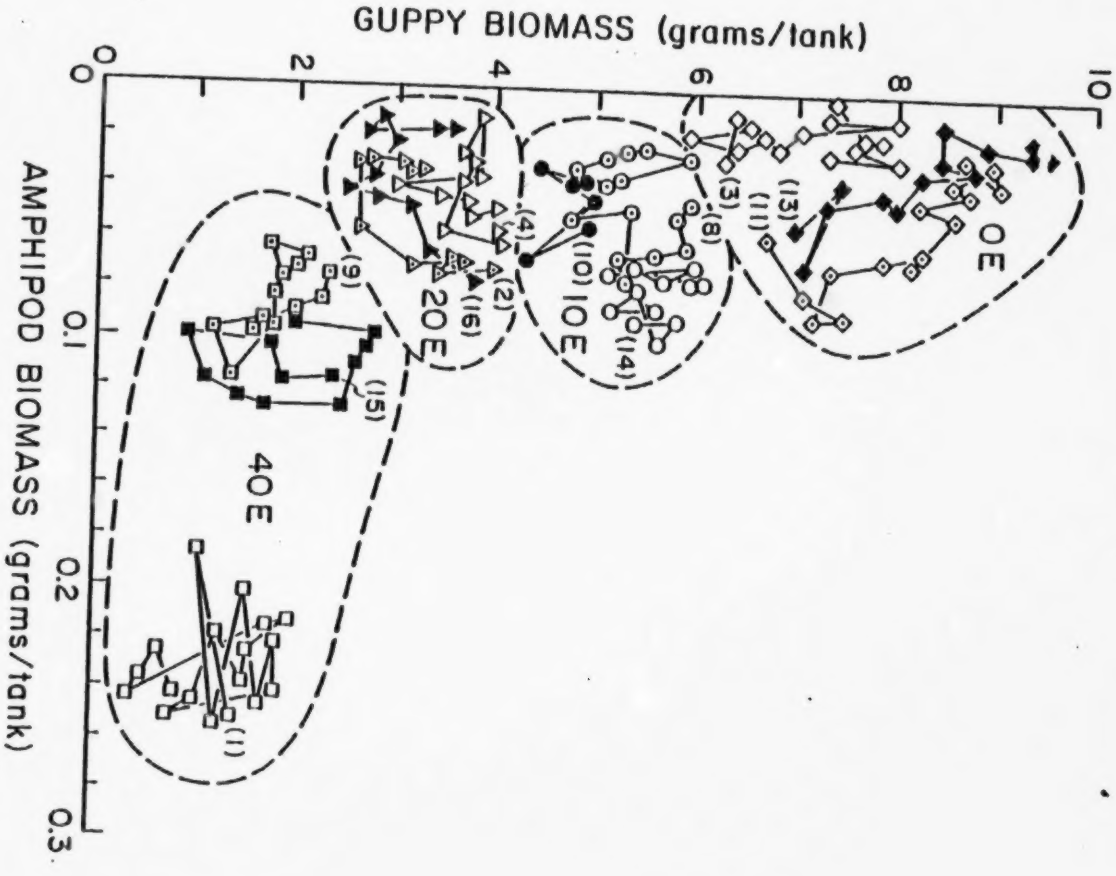
Prior to introduction of guppies into the laboratory ecosystems, amphipod populations did not establish near steady-states and reached maximum biomasses of 1.5 grams, the range at the time of guppy introduction being 0.1 to 1.0 grams. Introduction of guppies resulted in establishment of near steady-state amphipod biomasses that were much lower than the biomasses that existed prior to guppy introduction.

Snail populations were censused monthly beginning in October 1978. Consequently, in the four systems at the low level of habitat availability and energy input that were exposed to dieldrin, snail biomasses prior to dieldrin introduction were not determined. Represented in Figure 8 for the low level of habitat availability and energy input, is the relationship between near steady-state guppy and snail biomasses. An inverse relationship existed between near steady-state guppy and snail biomasses. Near steady-state snail biomass increased as a result of reduction in biomass of their guppy competitor brought about by increased exploitation.

Habitat availability and energy input rate were increased in eight of the laboratory ecosystems. In four of these systems planaria were systematically removed. In these systems, increased habitat and energy input shifted the near steady-state relationships between populations upward and to the right on each phase plane (Figures 9 and 10, see also Figure 1), this resulting in increased near steady-state biomasses of organic sediments, guppies, amphipods, and snails at each exploitation rate.

In systems where planaria were not removed, amphipod populations were driven to extinction by planaria predation (Finger, 1980; Woltering, 1980).

Figure 7. Phase plane representation of near steady-state guppy and amphipod population biomasses at low habitat availability and energy input rate. Guppy exploitation rates are indicated as ◇- 0, ○- 10, △- 20, and □- 40 percent. Populations were censused, and co-occurring population biomasses plotted at one-month intervals. Time on the phase plane begins at the system numbered point. After Woltering (1981).



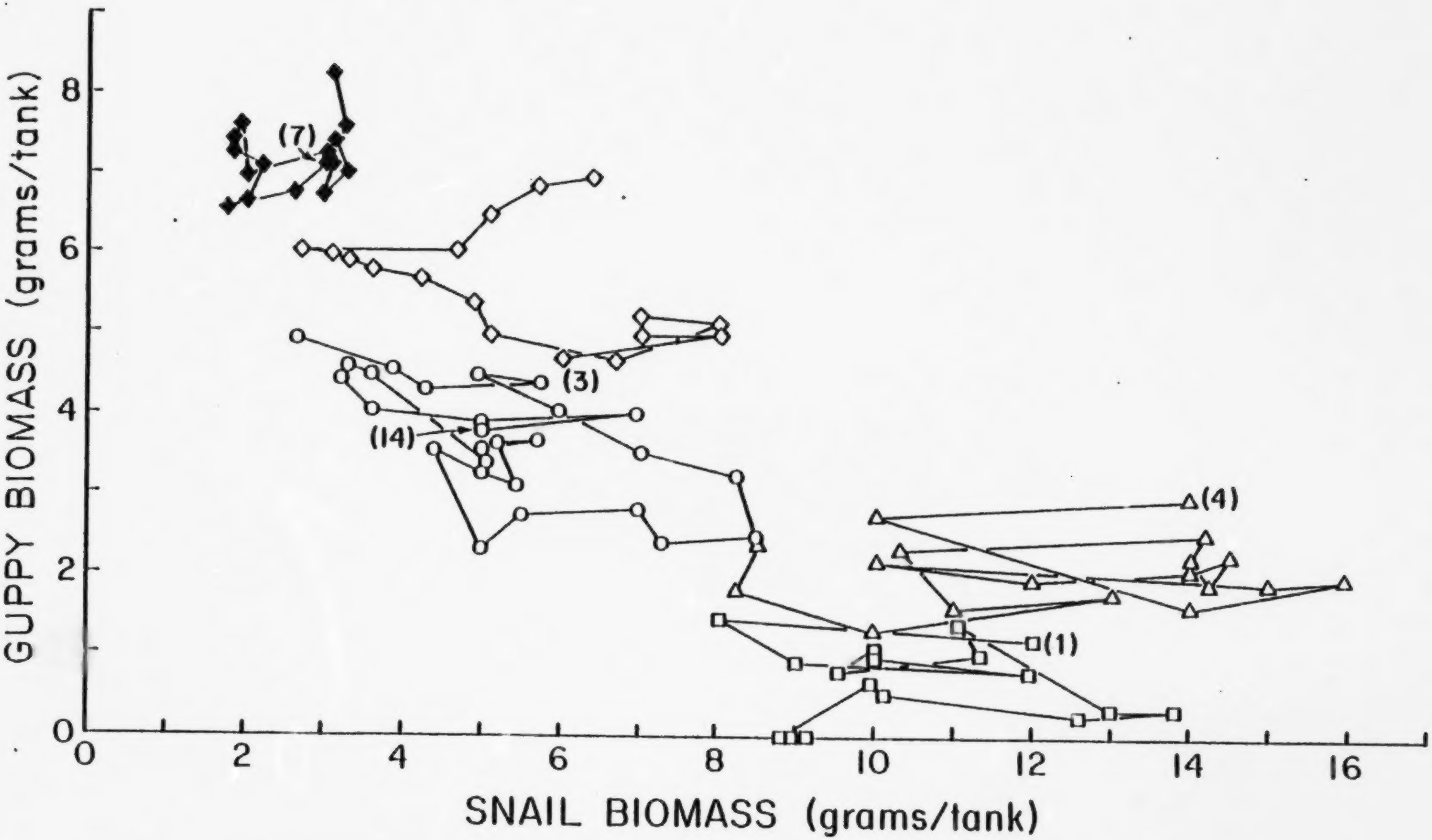


Figure 8. Phase plane representation of near steady-state guppy and snail population bomasses at low habitat availability and energy input (solid symbols), and at low energy input after introduction of dieldrin (open symbols). Snail populations were censused beginning in October, 1978. Guppy exploitation rate is indicated as ◇ -0, ○-10, △-20, and □-40 percent. Time on the phase plane begins at the system-numbered point. After Woltering (1981).

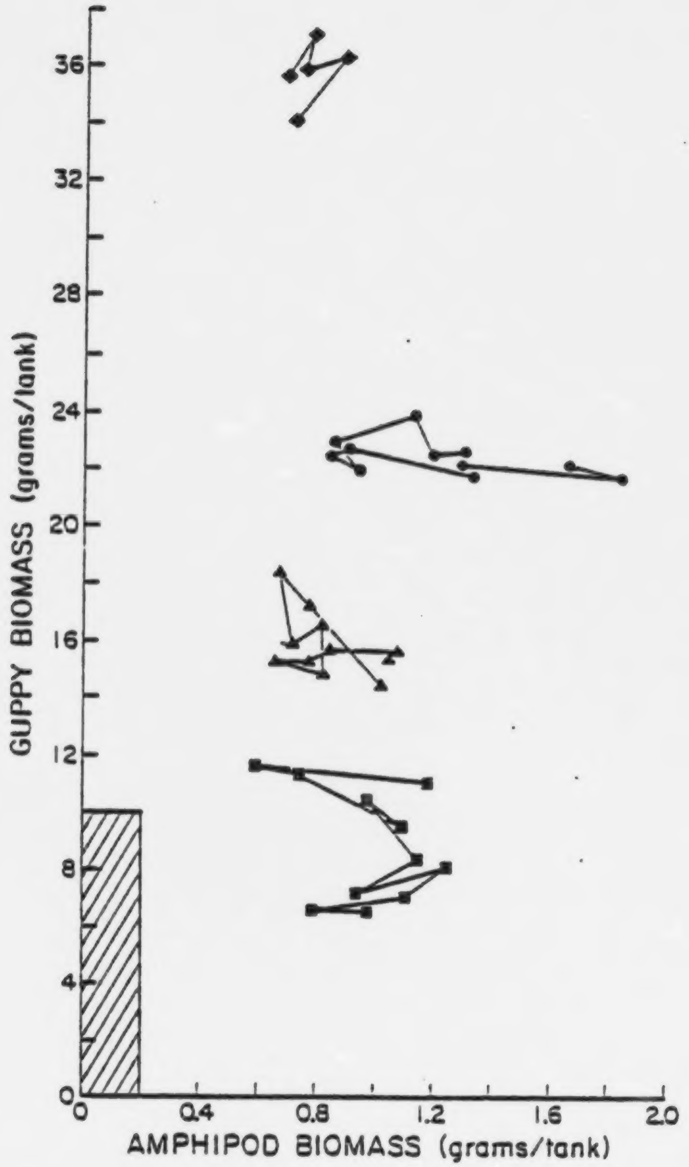


Figure 9. Phase plane representation of near steady-state guppy and amphipod population biomasses at high habitat availability and energy input rate. Hatched area indicates relative position of the systems at low energy input (see Figure 7). The trajectories between low and high energy input (Figure 5) have been removed to facilitate comparisons. Guppy exploitation rate is indicated as ◇- 0, ○- 10, △- 20, and □- 40 percent.

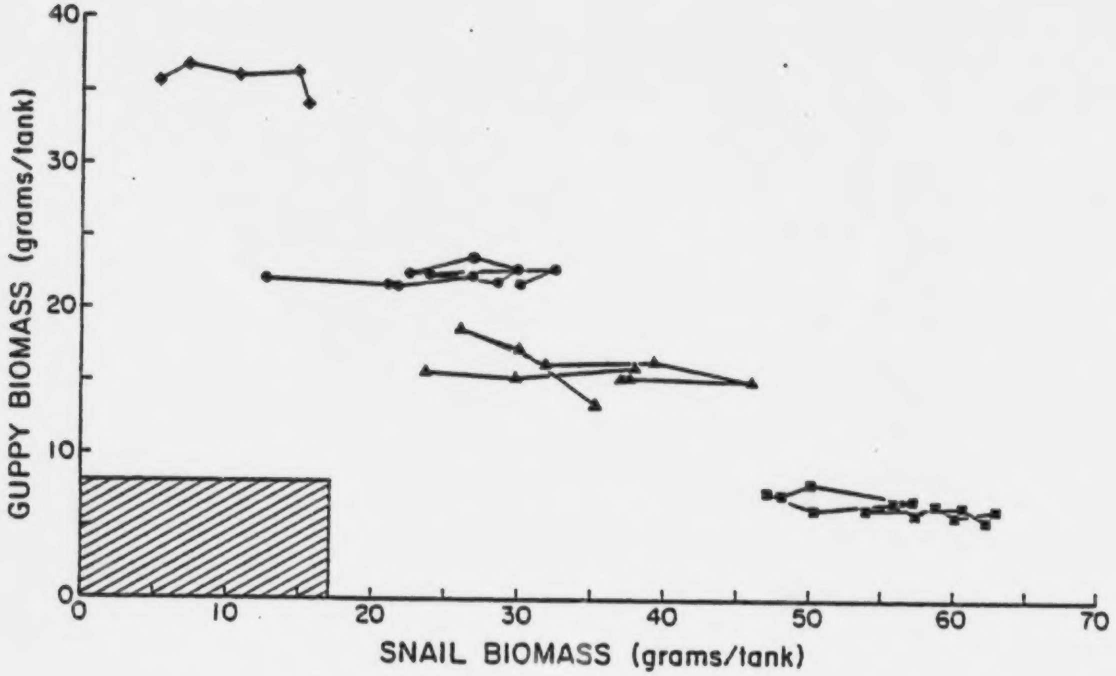


Figure 10, Phase plane representation of near steady-state guppy and snail population biomasses at high habitat availability and energy input. Hatched area indicates relative position of guppy and snail co-occurring biomasses at low energy input (see Figure 8). Guppy exploitation rate is indicated as ◇ - 0, ○ - 10, △ - 20, and □ - 40 percent. After Woltering (1980).

These systems have not yet established near steady-states and consequently will not be discussed in detail in this report. Presently guppy biomasses in these systems are not substantially different from those in systems where planaria were removed. Snail abiomasses in the systems with planaria at present appear to be somewhat greater than near steady-state snail biomasses in systems where planaria removal was instituted. Snails may be able to attain higher biomasses in systems with planaria because of the absence of their amphipod competitors (Woltering, 1980).

At the high level of habitat availability and energy input rate in systems where planaria were removed, increased exploitation rate resulted in reduction in ner steady-state guppy biomasses. Near steady-state amphipod biomasses appeared to be unaffected by changes in guppy biomass resulting from exploitation (Figure 9). The reasons for this are not yet well understood. Because of the large amount of rock substrate available as an amphipod refugium at the high habitat level, guppies may not have been able to effectively prey upon amphipods and thus had little direct impact on the population biomasses. But possible effects of competition with guppies and snails on amphipod abundances still need to be taken into account in explaining near steady-state biomasses.

As occurred at the low level of habitat availability and energy input rate, reductions in near steady-state guppy biomass brought about increases in the near steady-state biomass of their snail competitor (Figure 10). Thus, although their relative abundances varied, the dominant organisms in the laboratory ecosystems coexisted as competitors over a range of environmental conditions. The relative abundances of the competing populations were determined by rate of exploitation of the guppy population and level of habitat availability and energy input rate. At a particular habitat level and energy input rate, increased mortality of the guppy as a result of exploitation reduced its near steady-state biomass and enabled the snail to increase in near steady-state abundance, apparently because of reduced competition.

Organic sediment was taken to be representative of the food resource for which guppy, snail, and amphipod populations apparently competed. At the high level of habitat availability and energy input, organic sediments like amphipod biomass appeared to bear a slight inverse relationship to guppy biomass (Figure 11). At the low level of habitat availability and energy input rate, organic sediment biomass did not vary with changes in guppy, snail, and amphipod biomasses brought about changing exploitation rate (Figure 11). Apparently, organic sediment loss to predation and decomposition was approximately the same at all exploitation rates. Perhaps the amount of sediment consumed by a particular population varied according to the biomass of that population, which was indirectly determined by guppy exploitation rate. Increased exploitation rate caused a reduction in guppy biomass and probably consumption of sediments by guppies. But increases in snail and amphipod biomasses and perhaps increases in consumption of sediments by these populations occurred in accordance with reductions in guppy biomass and consumption. Thus, the outcome of the inverse relationship between guppy biomass and the biomasses of amphipods and snails was to maintain total consumption of organic sediments and sediment biomass relatively constant (Woltering 1980).

## System Response to Toxicant Introduction

At the low level of habitat availability and energy input, four systems, one at each exploitation rate, with the tightest near steady-state

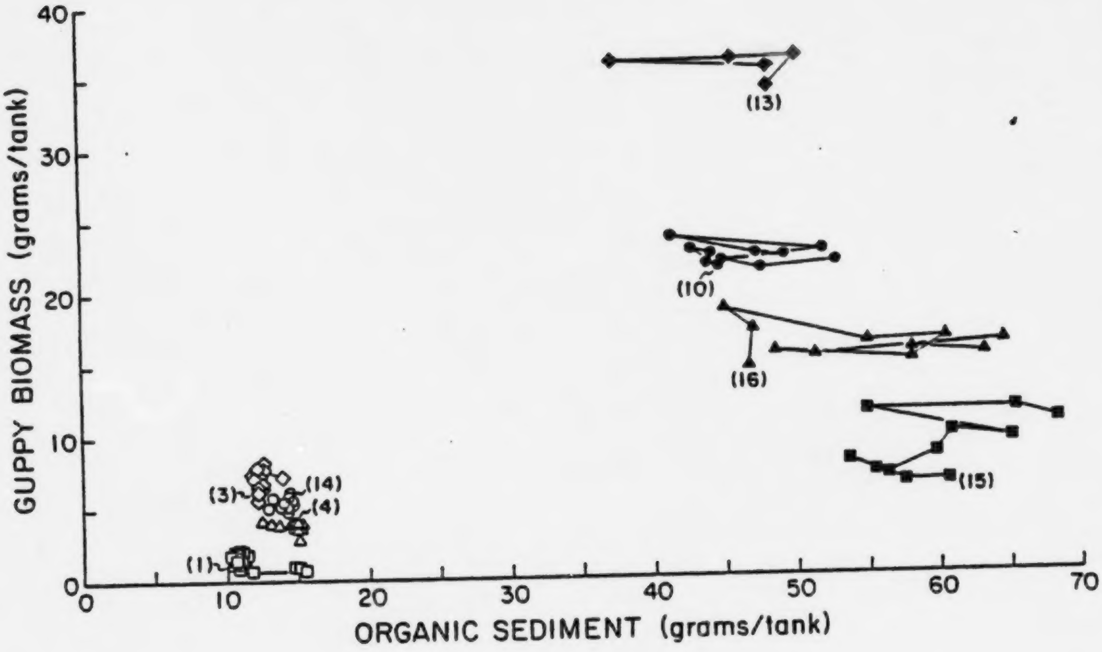


Figure 11. Phase plane representation of near steady-state guppy and organic sediment biomasses and the low (open symbols) and high (solid symbols) level of habitat availability and energy input rate. Guppy exploitation rates are indicated as ◇ - 0, ○ - 10, △ - 20, and □ - 40 percent.

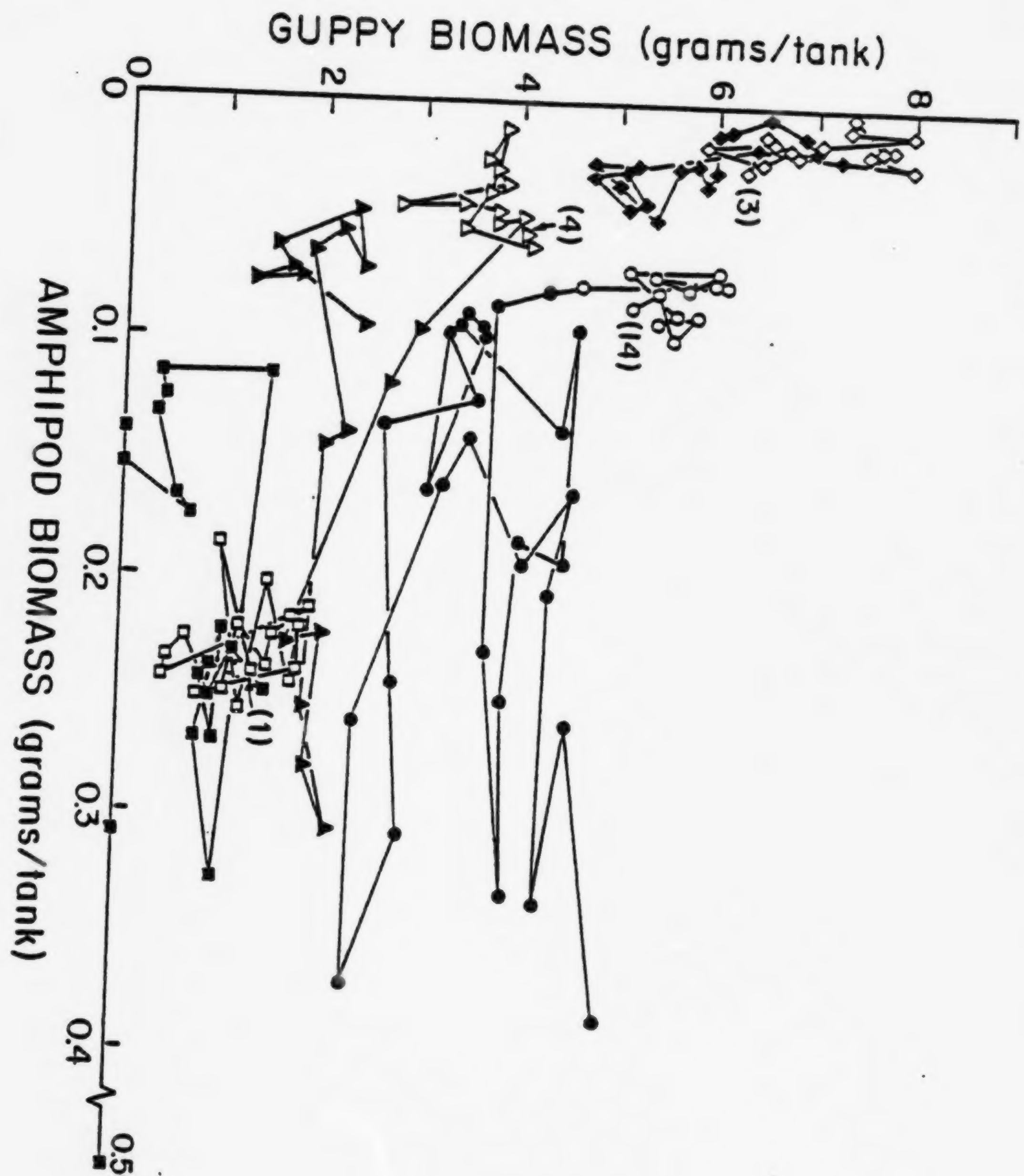
patterns of guppy and amphipod biomasses (systems 1,3,4,14) were selected for exposure to dieldrin. The four remaining systems (5,6,7, and 12), one at each exploitation rate, were kept unchanged at low energfy input. In the systems exposed to dieldrin, near steady-state guppy biomass was inversely related to near steady-state amphipod biomass prior to introduction of dieldrin (Figures 12 and 7). Near steady-state snail biomasses in these four systems, recorded after the introduction of dieldrin, was inversely related to near steady-state guppy biomass (Figure 8).

Experiments were conducted at our laboratory on the effects of dieldrin on individual organisms of the species present in the laboratory ecosystems to enable us to better explain the effects observed in the ecosystems. The 96 hour LC50 of newborn guppies was about 5 ppb and that of adult females about 20 ppb. Dieldrin concentrations of 1 ppb and 2 ppb affected age-specific growth, survival, and reproduction of guppies. The experiments on the effects of dieldrin on guppy life histories will be considered in more detail later in this report. The 96 hour LC50 for amphipods was about 50 ppb. Sublethal effects on amphipods could not be reliably determined, because of difficulties in maintaining individuals and populations in aquarium studies outside the laboratory ecosystems. Benthic microorganism populations when exposed to 150 ppb exhibited densities that were similar to those exhibited in the absence of dieldrin. Thus, a dieldrin concentration of 1 ppb in the laboratory ecosystems probably directly affected guppy survival, growth, and reproduction, as will be shown later in this report, and only indirectly affected other populations through its effects on guppies.

In general, the responses of the laboratory ecosystems to continuous exposure to dieldrin broadly conformed to the responses outlined in the Introduction (Figure 2). Responses were characterized by alterations in

Figure 12. Phase plane representation of dynamic and near steady-state guppy and amphipod population biomasses at low habitat availability and energy input prior to (open symbols) and after (solid symbols) continuous exposure to 1.0 ppb dieldrin. Guppy exploitation rates are indicated as ◇ - 0, ○ - 10, △ - 20, and □ - 40 percent guppy exploitation. At zero percent exploitation (system 3), guppy steady-state biomass was reduced by exposure to dieldrin but subsequently recovered to pre-dieldrin levels. At 10 percent exploitation (system 14), guppy biomass was reduced and amphipod biomass increased as a result of exposure to dieldrin. The system did not establish a near steady-state after dieldrin introduction. At 20 percent exploitation (system 4), guppies and amphipods established a new near steady-state after exposure to dieldrin. Guppy biomass was reduced and amphipod biomass was increased. At 40 percent exploitation (system 1), the guppy population went extinct after exposure to dieldrin. After Woltering (1981).

Figure 12.


GUPPY BIOMASS (grams/tank)
0
2
4
6
8
AMPHIPOD BIOMASS (grams/tank)
0
0.1
0.2
0.3
0.4
0.56
(1)
(3)
(4)
(4)
(14)

system structure and organization and were dependent upon exploitation rate. The effects ranged from perturbation and recovery at zero exploitation to extinction of the guppy population at 440 percent exploitation (Figure 12).

In he laboratory ecosystem at zero exploitation rate (System 3), after introduction of dieldrin there was an immediate and dramatic decrease in guppy biomass. Amphipod populations increased slightly as a result of the decrease in biomass of their guppy predator and competitor. Numerous male and adult female guppies died in the first few months after exposure. Such mortality was not apparent in the other three systems receiving dieldrin. At zero exploitation rate prior to dieldrin introduction, the guppy population maintained a relatively high density and apparently there was less food available per individual and slower individual growth than at higher exploitation rates (Figure 16). Thus, the fish were in relatively poorer condition and apparently were highly susceptable to dieldrin intoxication.

After the introduction of dieldrin, the system appeard to establish a new steady-state at a guppy biomass of about five grams and an amphipod biomass of about 0.4 grams (Figure 12, see also Figure 2). The system maintained this structure for about eight months. Although dieldrin was still being introduced, the system began to recover from toxicant perturbation, with guppy biomass gradually increasing and amphipod biomass decreasing. The structure of the recovered system eventually overlapped the near steady-state structure that existed prior to dieldrin introduction.

Evidently, the guppy population at zero exploitation was able to adapt evolutionarily to the presence of dieldrin and so recover from dieldrin perturbation. Natural selection could have altered the adaptive capacity of the populations by favoring those individuals that had the life history capacity to survive, grow, and reproduce most efficiently in the presence of dieldrin -- the so-called "resistant" individuals. These individuals exhibit life history patterns that are well adapted to the presence of dieldrin, thus enabling the population to increase in biomass while still being exposed to dieldrin.

In the laboratory ecosystem at 10 percent exploitation rate (system 14), exposure to dieldrin brought about a decrease in guppy biomass and an increase in amphipod biomass. However, the biomasses of both guppies and amphipods were highly variable and, after 28 months of continuous exposure to the pesticide, the system had failed to establish a near steady-state.

At the 20 percent exploitation rate (system 4), the system established a new near steady-state structure in the presence of dieldrin with near steady-state biomass of guppies about 46 percent lower and amphipod biomass about 50 percent higher than their near steady-state biomass prior to dieldrin introduction.

In the laboratory ecosystem at the 40 percent exploitation rate (system 1), guppy populations went extinct after 15 months of continuous exposure to dieldrin (see also Figure 2). For the first eight months after introduction of dieldrin, there were no obvious changes in the structure of the system. Guppy populations exploited at 40 percent maintained relatively low densities and often had size distributions with over 70 percent of the biomass in one large female. This sometimes resulted in significantly more or less than the prescribed 40 percent of the biomass being exploited in any given month. Over many months, however, mean exploitation rate was near 40 percent.

System 1 had been exploited by 77 and 82 percent in two of the 18 months prior to dieldrin introduction. In several months, the population recovered owing to density dependent increases in growth and reproduction of individual fish. After ten months of continuous exposure to dieldrin, system 1 was again "overexploited" at 75 percent (a one gram female). The population did not recover in the following five months and went extinct with the removal of a 0.2 and 0.5 gram female. The two fish carried a total of 42 eggs and embryos. For seven months prior to extinction, the number of newborn fish was at least 70 percent lower than the number of newborns present prior to dieldrin introduction. Thee had been no newborn fish present in the tank for three months prior to extinction. This suggests that not only changes in age structure of adults but also reduced survival of offspring accounted for reduction in offspring number. Offspring survival may have been reduced due to accumulation of dieldrin in eggs.

Over a one month period prior to extinction of the guppy population, amphipod biomass in system 1 was reduced from 0.33 to 0.12 grams as a result of planaria predation. Planaria were then removed from the system. It is unlikely that this lower amphipod biomass was influential in the decline of guppy biomass since, because of their low densities, amphipods are probably not a major prey of guppies.

In the laboratory ecosystem at the 40 percent exploitation rate into which dieldrin was not introduced (system 6), the guppy population has persisted for 47 months, up to the present time. Guppies in this system are also subjected to occasional "overharvest," this further supporting the conclusion that guppy population extinction in system 1 resulted from exposure to dieldrin.

After extinction of guppies, amphipod biomass increased, reaching levels that the populations had not attained since guppies were introduced. In addition, behavioral changes occurred, the amphipods moving more freely throughout the tank rather than restricting their movement primarily to the rock nests. Since snail populations were not censused prior to dieldrin introduction, effects on snail biomass could not be determined.

## Guppy Population Structure and Organization Near Steady State

Guppy populations play an integral role in the organization of the laboratory systems, functioning as a dominant predator and competitor and being subjected to exploitation simulating fishing. At each level of habitat availability and energy input, changes in guppy biomass resulting from exploitation apparently brought about major changes in the biomass of other populations composing the communities. Guppy populations were directly affected by dieldrin, their response to the pesticide being dependent upon the rate at which they were exploited.

Changes in guppy population biomass can be operationally explained in terms of population biomass gains from production (growth and reproduction) and losses to mortality including yield to exploitation. Survival, growth, and reproduction are integral parts of the life history patterns of individual organisms. Individuals develop different life history patterns under different sets of environmental conditions, thus maintaining concordance with these conditions. Developmental as well as evolutionary changes in life history adapt populations to persist and underlie changes in population production, yield, and biomass brought about by changes in exploitation rate, habitat and energy level, and dieldrin.

### Guppy Population Biomass, Production, and Yield Near Steady-State

Mean near steady-state guppy biomasses corresponding directly to a near steady-state guppy trajectory patterns on predation and competition phase planes, (Figure 6-12) are shown in Figure 13. At each level of habitat availability and energy input, mean guppy biomass decreased as the level of exploitation increased. Dieldrin led to a decrease in mean guppy biomass of approximately 24 percent at zero exploitaton (followed by an eventual recovery), 32 percent at ten percent exploitation, 46 percent at twenty percent exploitation, and 100 percent (eliminating the guppy population) at forty percent exploitation. Increased level of energy input and habitat availability resulted in an increase in mean guppy biomass.

To maintain guppy population biomass near steady-state, production, or the rate of elaboration of tissue through growth and reproduction, must equal the rate of loss of tissue to yield and natural mortality. At the low level of habitat availability and energy input, very little natural mortality occurred in populations exploited at 10, 20, and 40 percent, and consequently near steady-state production is approximately equal to near steady-state yield in each population. At the 0 percent exploitation rate, since yield was zero, near steady-state natural mortality rate must equal near steady-state production. Observed near steady-state natural mortality of fish above the newborn size in the four systems that received dieldrin were, before and after dieldrin introduction, 0.17 and 0.31 grams per month for zero exploitation, 0.01 and 0.00 for 10 percent, 0.0 and 0.08 for 20 percent, and 0.00 and 0.00 for 40 percent exploitation.

Changes in the magnitudes of production and yield curves represent changes in the productivity of the system for guppies. Increasing habitat availability and energy input rate increased system productivity, while exposure to dieldrin reduced the productivity of the systems for guppies

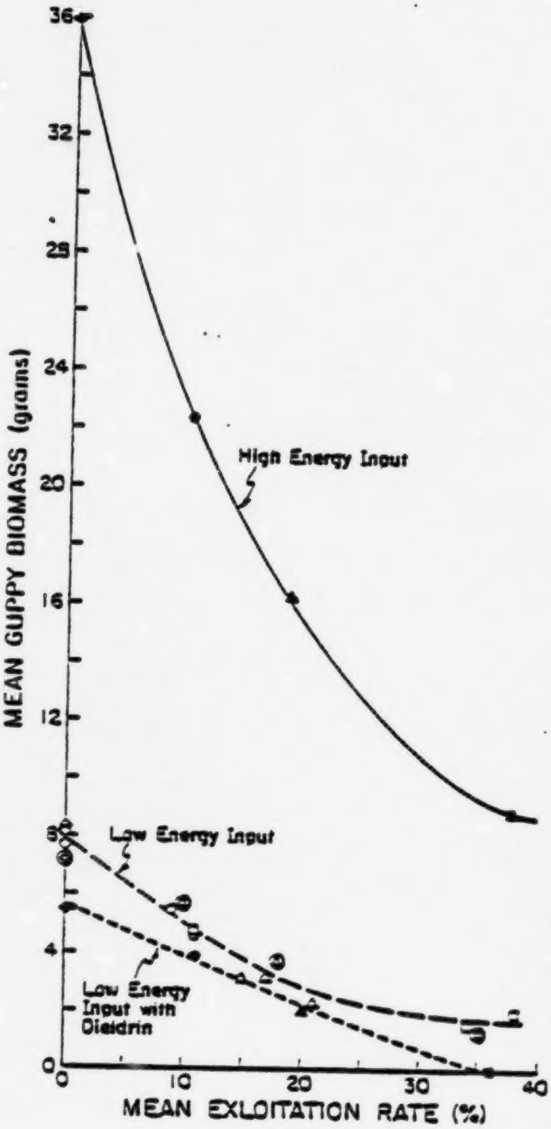


Figure 13. Mean guppy population biomasses near steady-state as a function of the mean exploitation rate. Guppy exploitation rates are indicated as ◇ - 0, ○ - 10, △ - 20, and □ - 40 percent. Circled open symbols are low energy input systems into which dieldrin was introduced. Curves are fit by eye.

(Figure 14); see also Figure 3). Guppy production at high habitat availability and energy input was not determined. The relative position that such a curve would occupy is shown.

Increasing exploitation rate resulted in reduction in guppy biomass and essentially shifted production and yield values from right to left along the dome-shaped curves. Increased habitat and energy input increased guppy food resources, this resulting in increased guppy biomass, production, and yield at each exploitation rate. Shift to the right in the relationships between guppy biomass and the biomass of their food (Figures 9 and 10) characterized the increase in productivity making possible the increased magnitude of guppy production and yield curves.

At low habitat and energy input, exposure to dieldrin reduced the magnitude of guppy production and yield curves. Dieldrin directly affected only the guppy populations and, as will become apparent, altered life history patterns by reducing size-specific growth and reproduction, as well as survival, this accounting for decreased guppy biomass and reduced magnitude of production and yield curves.

## Guppy Size-Specific Growth and Fecundity Near Steady State

The life histories of individual organisms include the patterns of growth and reproduction they manifest when exposed to different sets of environmental conditions. Guppy size-specific relative growth rate near steady-state was affected by exploitation rate, exposure to dieldrin, and level of habitat availability and energy input. Changes in these environmental conditions altered not only life history patterns but also population density and community structure. Growth was determined as change in body weight per unit of body weight per month. Elaboration of somatic tissue was not separated from elaboration of reproductive products in mature fish.

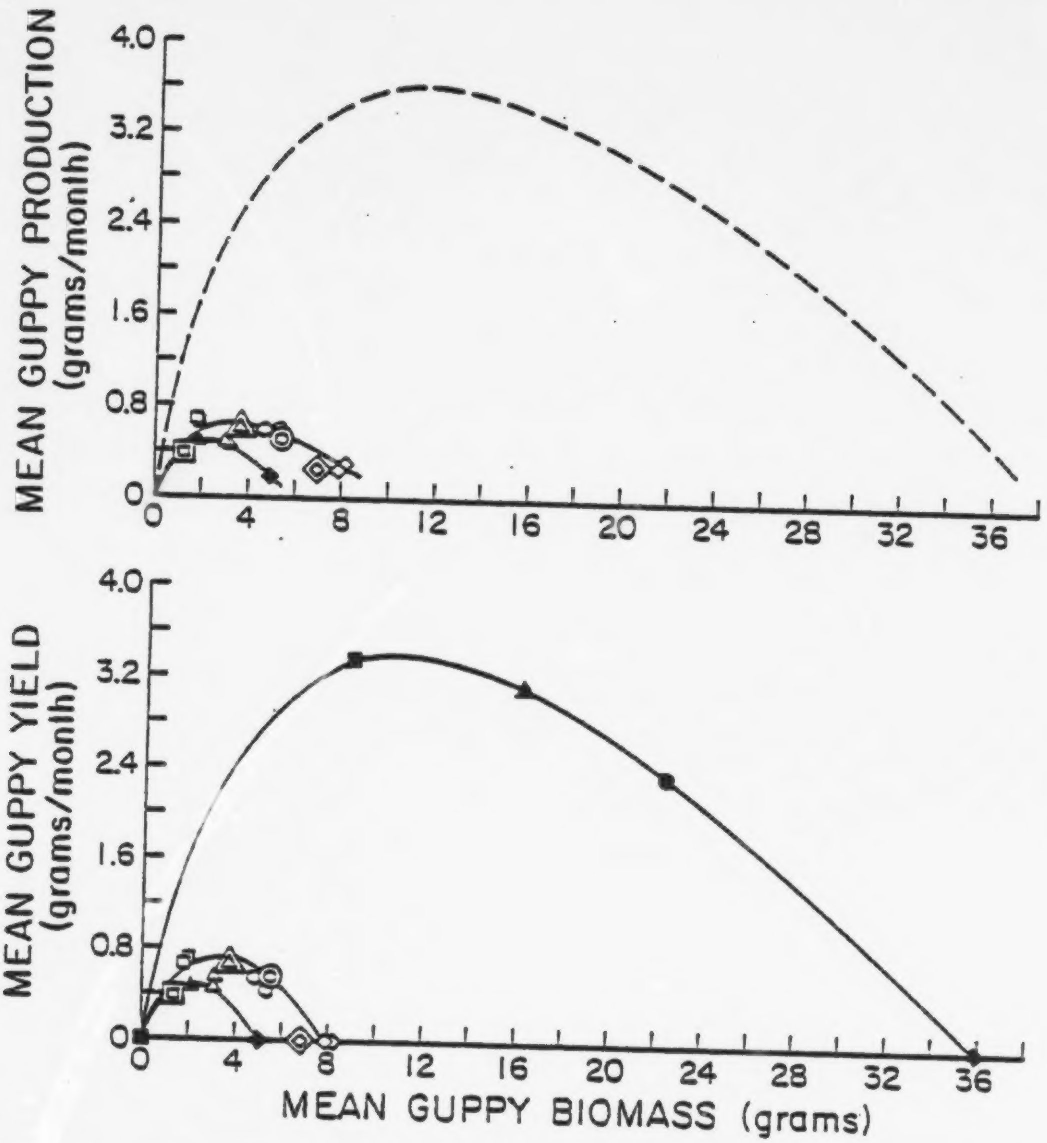


Figure 14. Mean near steady-state guppy population production (upper axis) and yield (lower axis) as a function of mean near steady-state population biomass. Guppy exploitation rates are indicated as ◇ - 0, ○ - 10, △ - 20, and □ - 40 percent per month. Open symbols are production and yield for low energy input systems; the four circled open symbols are low energy input systems into which dieldrin was introduced. The lowest curves represent near steady-state production and yield after introduction of dieldrin at the low level of habitat availability and energy input. The highest curves represent production and yield at the high level of habitat availability and energy input. Production at high habitat and energy input was not able to be determined, but the relative position that such a curve would occupy is shown by the dashed line.

Elaboration of reproductive products occurs continuously in mature guppies. Male guppies reached sexual maturity near 15 millimeters and their growth after that was often negligible.

Due to the much greater densities of fish at the high level of habitat and energy input, individual guppies could not be realiably followed from month to month. Consequently, size-specific relative growth rates and production could not be determined.

At each exploitation rate, relative growth rate decreased as the fish grew larger (Figure 15). Growth rates of immature (newborn, 10-14 mm) and mature fish of a given size was density-dependent, or related to population biomass and consequently to exploitation rate (Figures 15 and 16). The highest growth rates occurred at 40 percent exploitation where population biomass was lowest, and the lowest growth rates occurred at zero exploitation where population biomass was greatest.

In general, at both the high and low level of habitat availability and energy input, size-specific fecundity appeared to be density-dependent, the highest fecundity occurring at 40 percent exploitation and the lowest fecundity occurring at 10 percent exploitation (Figures 17 and 18). Fecundity determinations were made on exploited females and, therefore, fecundity estimates are not available for females in populations exploited at zero percent. Similar density-dependent effects on fecundity in exploited guppy populations were found by Liss (1974).

At the low level of habitat availability and energy input rate (Figure 17), there was overlap in fecundity relationships between systems exploited at different rates, making interpretation of fecundity data rather tenuous. Average fecundity data for the four systems at each exploitation rate suggested that size-specific fecundity was related to exploitation rate and population density. At each exploitation rate, size

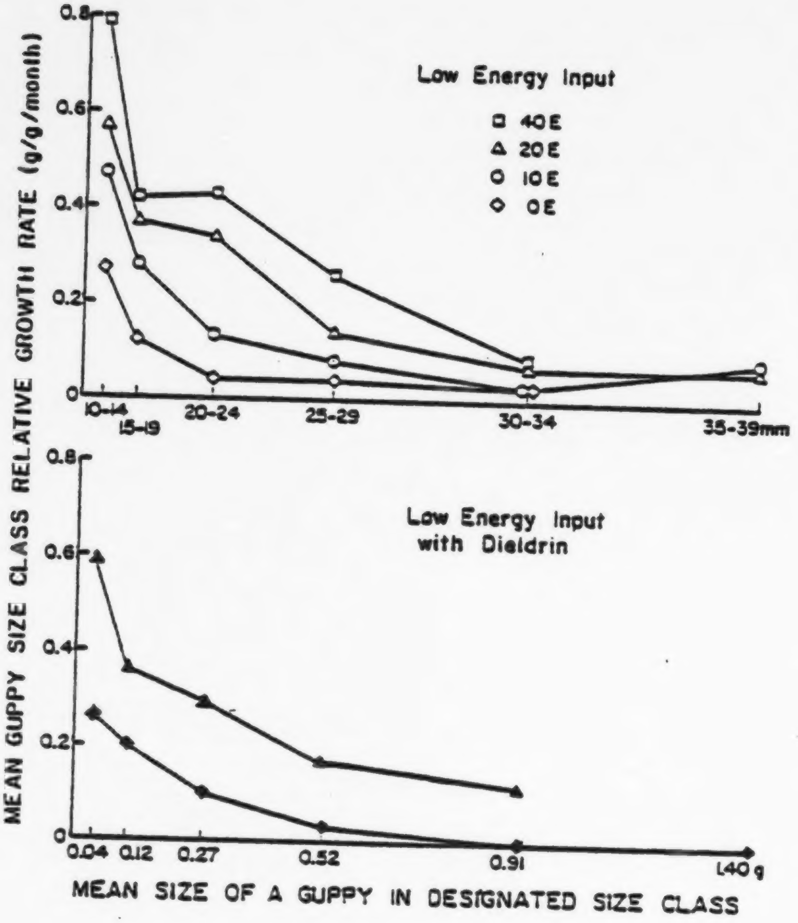


Figure 15. Guppy mean relative growth rate near steady-state for the systems at the low level of habitat availability and energy input before (open symbols) and after (solid symbols) introduction of dieldrin. Guppy exploitation rate is indicated as ◇-0, ○-10, △-20, and □-40 percent. Fish size is expressed as length (mm) and as mean weight (grams) for each size class. The population exploited at 10 percent did not establish a steady-state after introduction of dieldrin and, consequently, growth rates of individuals from this population are not shown. The population exploited at 40 percent went extinct after dieldrin introduction and growth rates are zero. After Woltering (1980).

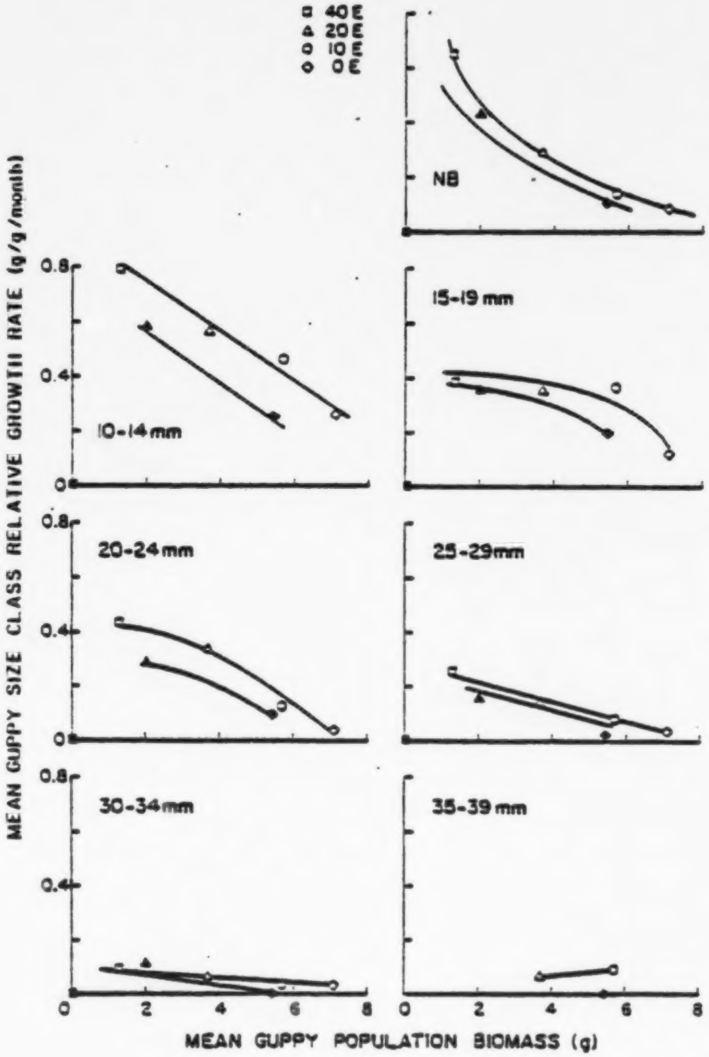


Figure 16. Guppy mean relative growth rate near steady-state as a function of near steady-state population biomass at the low level of habitat availability and energy input. Guppy exploitation rate is indicated as ◇ - 0, ○ - 10, △ - 20, and □ - 40 percent. Open symbols represent growth rate prior to introduction of dieldrin and solid symbols represent growth rate after exposure to dieldrin. The population exploited at 10 percent did not establish a steady-state after introduction of dieldrin and consequently growth rates of individuals from this population are not shown. The population exploited at 40 percent went extinct after dieldrin introduction and growth rates are zero. Not all populations had fish in the 35-39 mm size class. Curves were fit by eye.

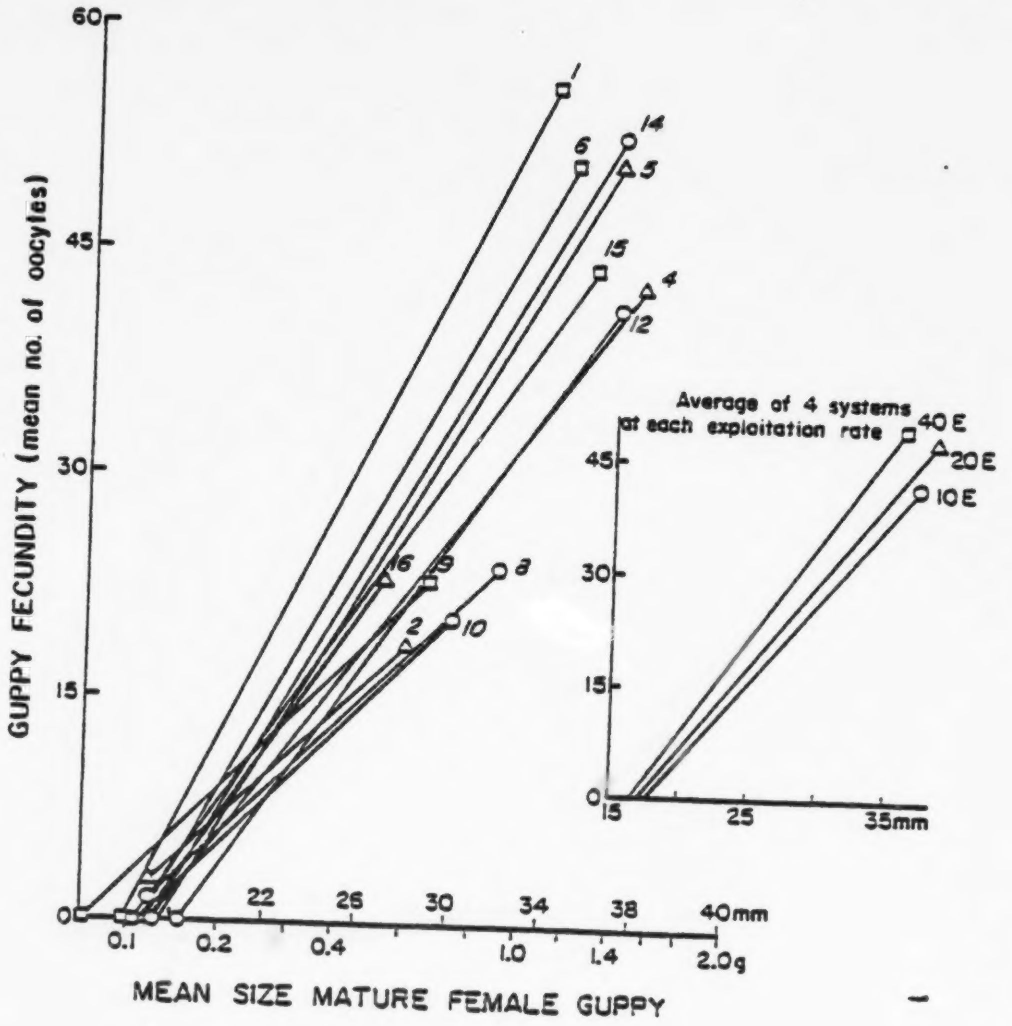


Figure 17. Guppy fecundity (mean number of eggs and embryos carried by an exploited female of given size) near steady-state for laboratory ecosystems at the low level of habitat availability energy input. Guppy exploitation rate is indicated as ○ - 10, Δ - 20, and □ - 40 percent. Inset shows average fecundity of the fours systems at each exploitation rate. A linear regression was fit to the data for each system; r values were between 0.85 and 0.99. After Woltering (1981).

specific fecundity was greater in fish at the high level of habitat availability and energy input than in fish at low habitat and energy input (Figure 18), this probably reflecting the greater availability of food.

Information on near steady-state relative growth rates and fecundities of fish exposed to dieldrin is limited to those exploited at 0 and 20 percent. The guppy population exploited at 10 percent never established a well-defined near steady-state after exposure to dieldrin. The steady-state of the population exploited at 40 percent after exposure to dieldrin was extinction. Thus, the effect of dieldrin on the relationshp between relative growth rate and population biomass is only suggestive and is inferred from information on populations exploited at 0 and 20 percent.

Dieldrin apparently reduced the relative growth rates of juvenile fish and small mature females up to 24 mm in length (Figure 16). For each of these size classes, the relationship between relative growth rate and population biomass was shifted downward, indicating that fish in populations of a given biomass grow more slowly after exposure to dieldrin. Since so few fish reached the larger size groups, it is possible that effects of dieldrin on growth of larger fish was undetected.

Dieldrin reduced size-specific fecundity of mature female guppies, this contributing to reduction in relative growth rate (Figure 19). Since growth rate of immature fish 10-14 mm in length was decreased, dieldrin evidently decreased somatic growth as well as elaboration of reproductive products.

The relationship developed at 40 percent exploitation rate after exposure to dieldrin is a non-steady-state relationship that was fit to fecundity information collected during the six months prior to extinction

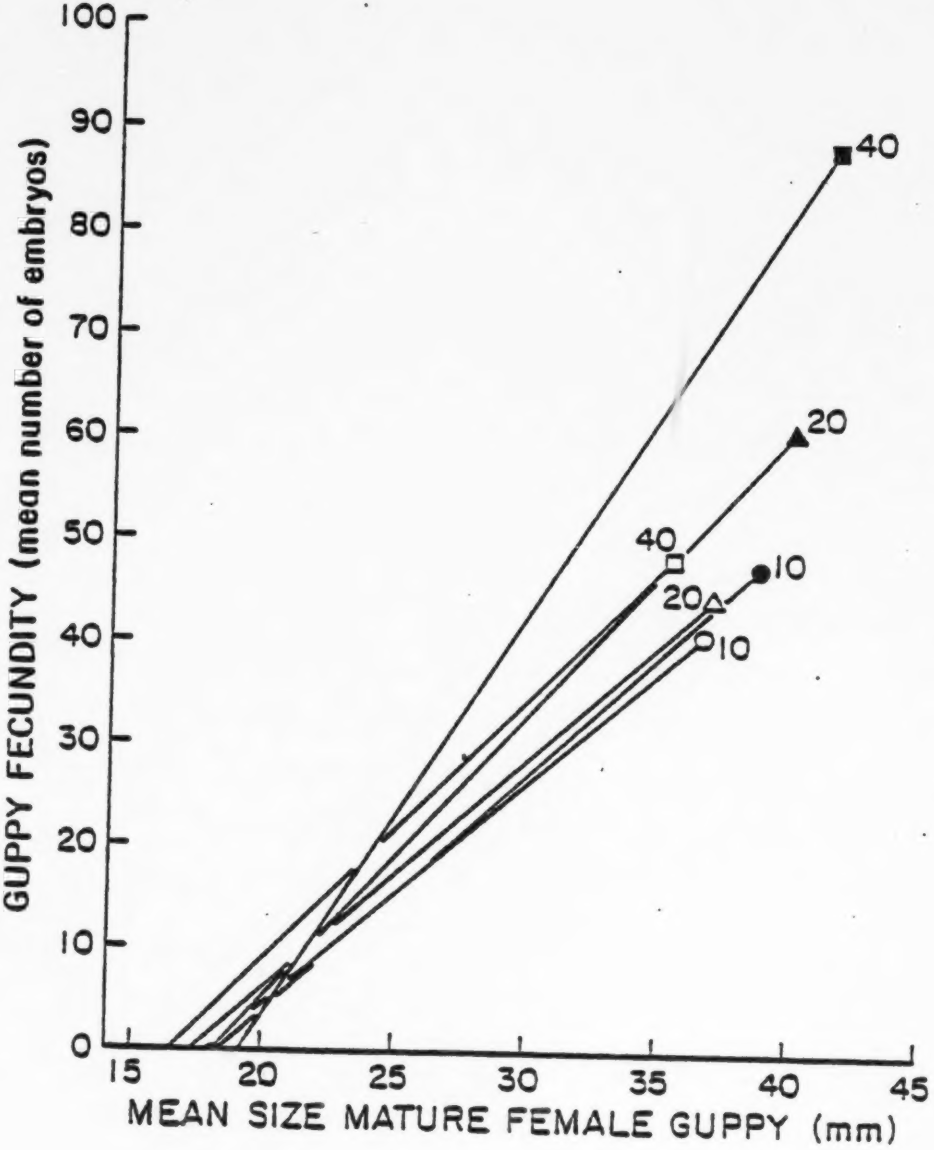


Figure 18. Guppy fecundity (mean number of eggs and embryos carried by an exploited female of a given size) near steady-state at low (open symbols) and high (solid symbols) levels of habitat availability and energy input. A linear regression was fit to the data for each system; r values were between 0.85 and 0.99. Guppy exploitation rates indicated as ○ - 10, △ - 20, and □ - 40 percent. Relationships at the low level of habitat and energy input are identical to average fecundity relationships shown in the inset in Figure 17.

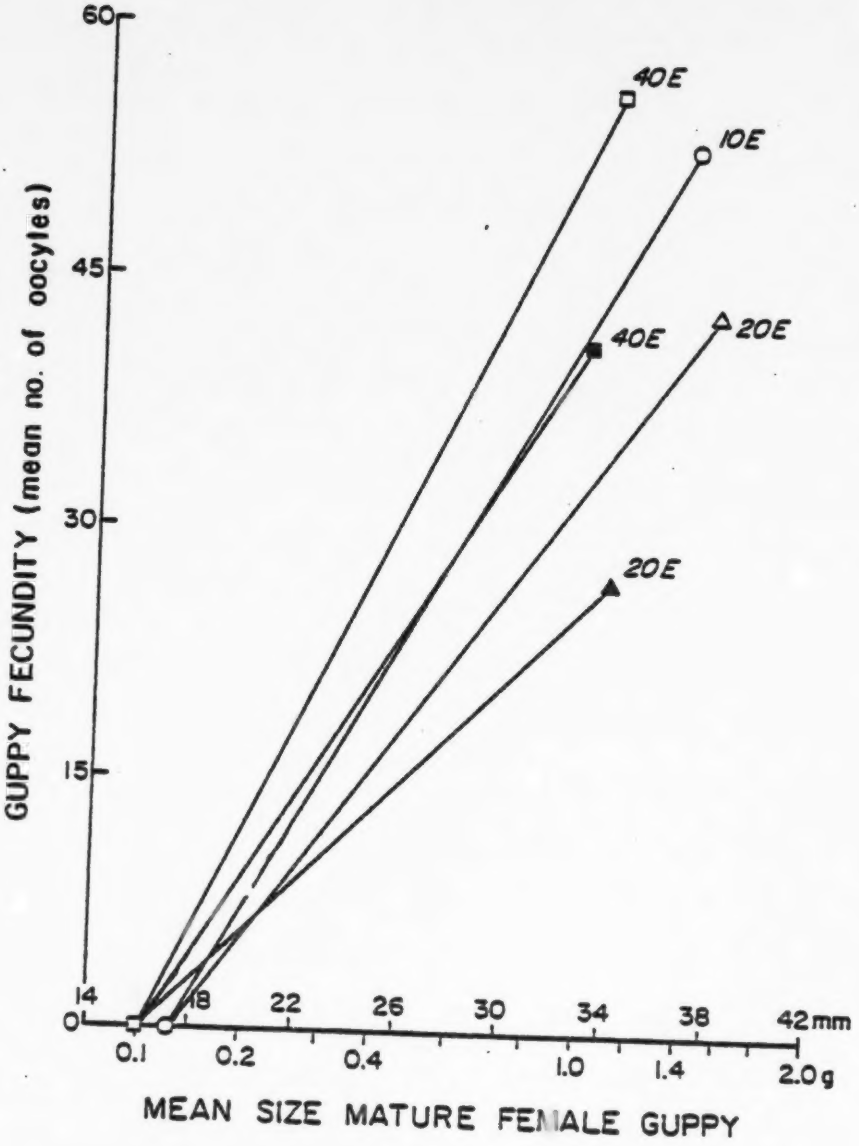


Figure 19. Guppy fecuncity (mean number of eggs and embryos carried by an exploited female of given size) in ecosystems at the low level of habitat availability and energy input before (open symbols) and after (solid symbols) dieldrin introduction at 10, 20, and 40 percent exploitation rates (system 2-40E, system 4-20E, system 14-10E). A linear regression was fit to the data for each system; r values were between 0.85 and 0.99. All relationships except that at 40 percent exploitation after dieldrin introduction were determined when the systems were near steady-state. The guppy population exploited at 40 percent went extinct after exposure to dieldrin. The fecundity relationship shown here was constructed from size-fecundity information obtained over the seven months just prior to extinction (see Figure 12). After Woltering (1981).

when population biomass was declining (see Figure 12). It indicates that reduced fecundity as well as poor survival of newborn fish and probably also reduced growth were all responsible for bringing about population extinction.

Changes in conditions in the environments of the laboratory communities such as exploitation rate, habitat availability and energy input, and exposure to a toxicant brought about changes in guppy life history pattern, population density, and community structure. That particular guppy life history patterns can be associated with particular community structures is evidenced at least at low habitat and energy input levels. Increasing exploitation rate resulted in reduction in length of life (as a result of increased fishing mortality) and apparent density-dependent increases in size-specific growth rate and fecundity. Exposure to dieldrin altered life history patterns in that it reduced newborn survival, size-specific growth rates, and fecundity. Some of these kinds of effects on guppy life history patterns were also observed in separate aquarium experiments more like simple toxicity tests.

## Cohort Size-Specific Biomass, Production, and Yield Near Steady-State

Mean near steady-state biomass of each size class of guppies at the low level habitat availability and energy input is shown in Figure 20. So long as the population is at steady-state, the pattern of change of size class biomass from newborn to the largest female can be taken to describe changes in biomass of a cohort as it moves through size classes. The sum of the mean near steady-state biomasses of all size classes equals mean near steady-state population biomass.

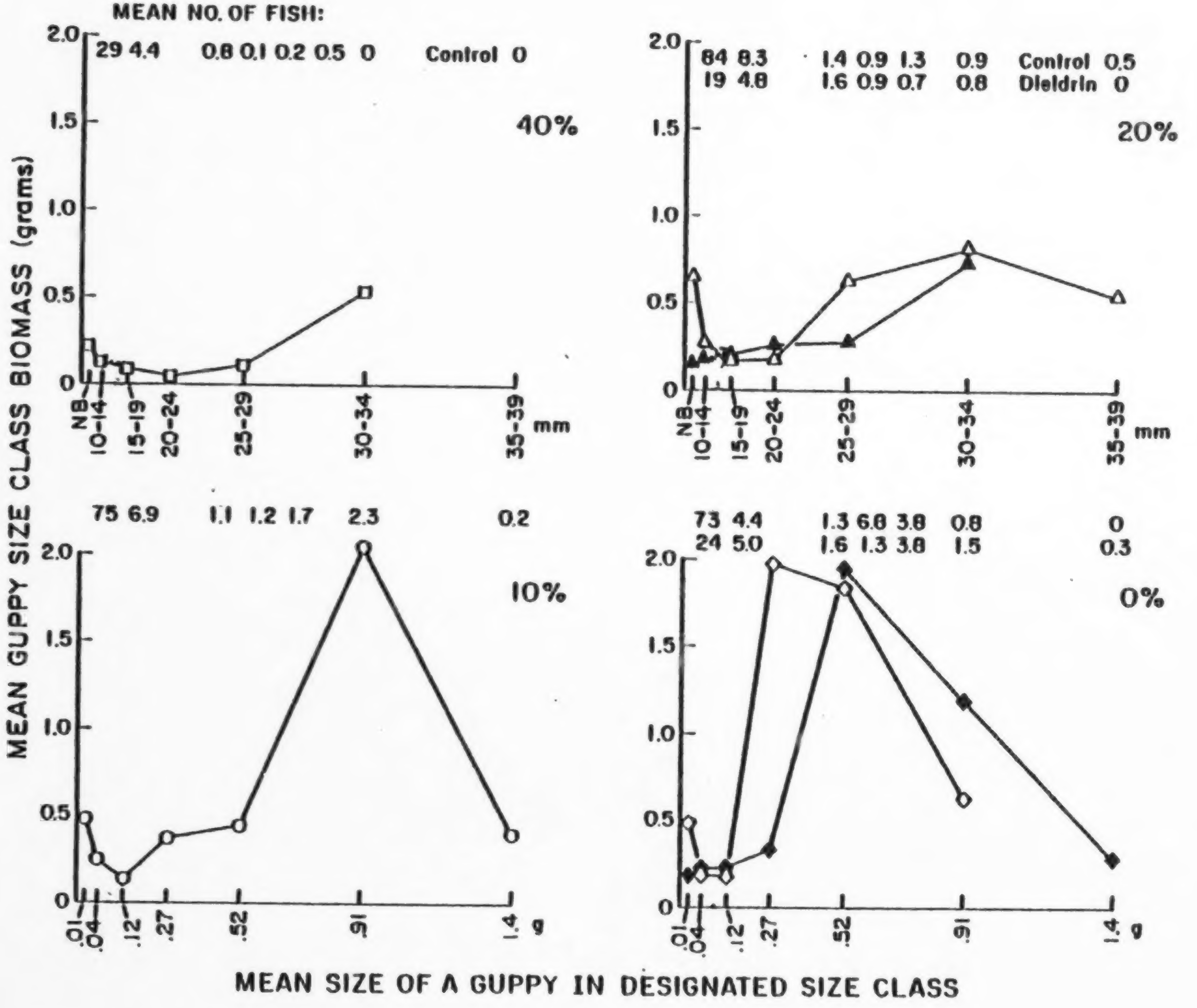


Figure 20. Guppy size class mean biomasses near steady-state for the four low habitat availability and energy input systems ( ◇- 0, ○- 10, △ - 20, and □ - 40 percent guppy exploitation) before (open symbols) and after (solid symbols) dieldrin introduction. Size is expressed both as length (mm) and as weight (grams) for each size class. After Woltering (1981).

At each exploitation rate, changes in cohort biomass are determined by the rate that a cohort elaborates biomass through production and the rate that it looses biomass as yield and natural mortality. When production is greater than yield and natural mortality, cohort biomass increases and when production is less than yield and natural mortality the biomass of the cohort declines. If the cohort is exploited at the same rate at all ages, maximum yield is obtained from the cohort when its biomass is greatest.

At all exploitation rates, size class biomass decreased somewhat between the newborn and 10-14 mm (0.12g) size class probably as a result of high mortality of young, at least in part resulting from cannibalism. Size class biomass was greatest in the 20-34 mm size class, except at zero exploitation where high density and relatively slow growth resulted in few guppies reaching larger sizes.

Production of fish in each size class can be determined as the product of relative growth rate (Figure 16) and biomass (Figure 20) of the size class. Size class production is represented in Figure 21 as a function of mean near steady-state population biomass. The yield of each size class as a function of population biomass is shown in Figure 22. At each exploitation rate, the sum of the mean near steady-state production and yield values of all size classes equals mean near steady-state population production and yield, respectively. Production and yield relationships for each size class, as well as total population production and yield (Figure 14), are dome-shaped curves. Families of production and yield curves exist for each size class, with exposure to toxicants altering the magnitudes of these curves.

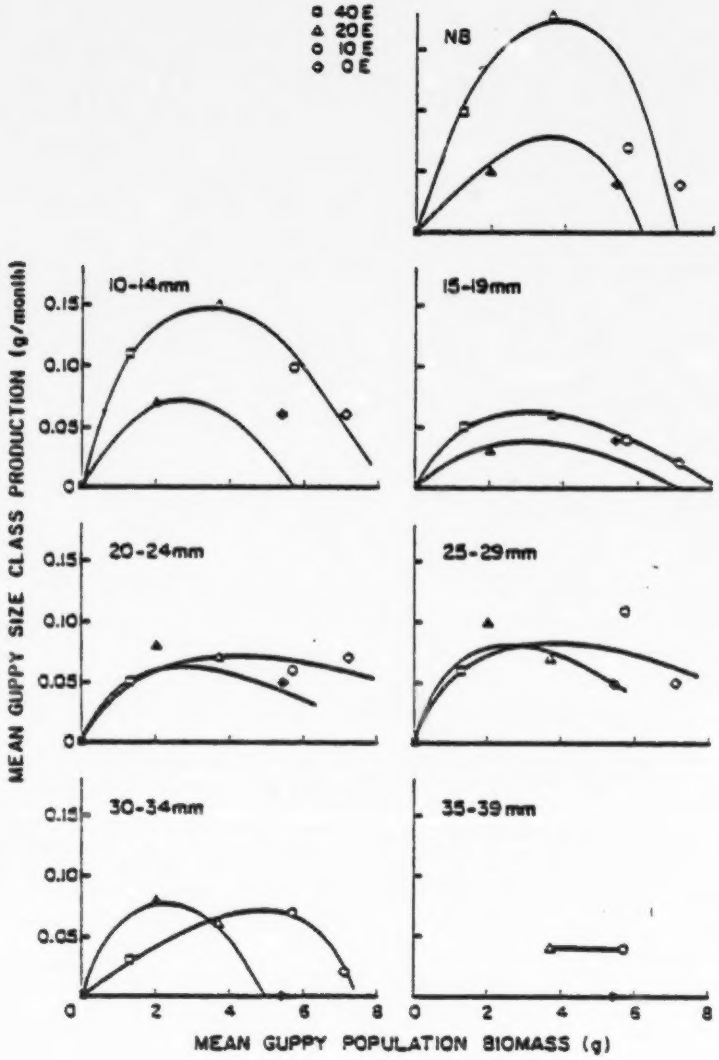


Figure 21. Guppy size class mean production near steady-state as a function of near steady-state population biomass for four low habitat availability and energy input systems (◇ - 0, ○ - 10, △ - 20, and □ - 40 percent) before (open symbols) and after (solid symbols) dieldrin introduction. The population exploited at 10 percent did not establish a steady-state after introduction of dieldrin and size class production from this population is not shown. The population exploited at 40 percent went extinct after dieldrin introduction and size class production is zero. Curves were fit by eye. After Woltering (1981).

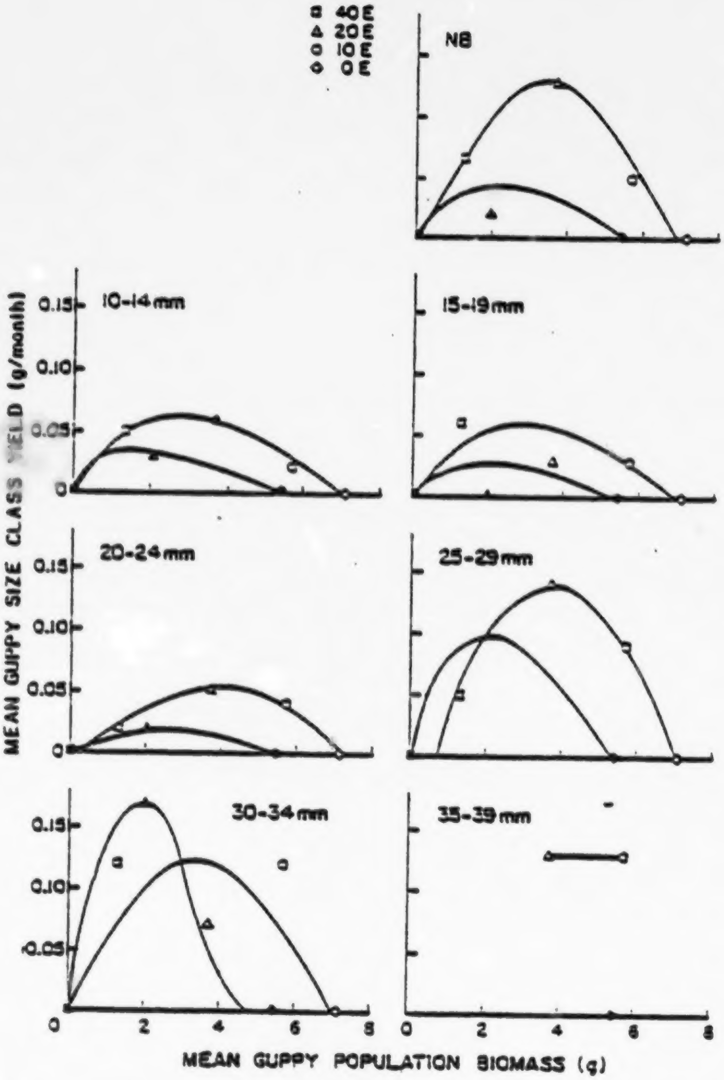


Figure 22. Guppy size class mean yield near steady state as a function of near steady-state population biomass for four low habitat availability and energy input systems ( ◇- 0, ○- 10, △ - 20, □ - 40 percent) before (open symbols) and after (solid symbols) dieldrin introduction. The population exploited at 10 percent did not establish a steady-state after introduction of dieldrin and size class yield from this population is now shown. The population exploited at 40 percent went extinct after dieldrin introduction and size class yield is zero. Curves were fit by eye. After Woltering (1981).

Size class production is greatest in the smaller size classes where organisms are growing most rapidly (Figures 15 and 16). Although size class biomass is large in the older size classes (Figure 20), growth rate has been so reduced that production, the product of growth rate and biomass, is low. Size class yield is greatest in the larger size classes where size class biomass reaches a maximum.

Thus, a pattern of guppy cohort dynamics becomes apparent. When a cohort passes through the smaller size classes, individual relative growth rate and cohort production are high and yield and other losses to natural mortality, after the newborn stage, are relatively lower and, in general, cohort biomass increases. As the cohort passes through successively larger sizer classes, relative growth rate and production decline and yield increases, the cohort reaching its maximum biomass where cohort production equals cohort yield (and other mortality). At this point cohort yield is maximum. In the largest size classes, cohort yield is greater than cohort production and cohort biomass declines. Even though cohort production may differ from cohort yield (and other losses) in a particular size group, total production of the cohort throughout its lifetime must equal total cohort losses to yield and natural mortality to maintain the population at steady-state.

It is just such dynamic patterns of cohort biomass, production, and yield that underlie steady-state population biomass, production, and yield and represent an important aspect of population structure and organization. And it is the life history patterns -- dynamic development patterns -- of individual organisms -- that underlie and determine dynamic patterns of cohort biomass, production, and yield under different sets of environmental conditions.

At the low level of habitat availability and energy input rate, dieldrin reduced the magnitude of guppy population production and yield (Figure 14). This decrease can be accounted for primarily through reduction in production and yield of immature and small mature females (Figures 21 and 22). These reductions resulted from decreases in both the biomasses and relative growth rates of these size classes (Figures 16 and 20).

### Effects of Dieldrin on Guppy Life History Patterns Determined in Aquarium Experiments

The impact of dieldrin on the life history patterns of guppies was determined in aquarium experiments more like simple toxicity tests. The intent was to relate the results of these experiments to effects on guppy life history patterns, population dynamics, and community structure and organization observed in the laboratory ecosystems and to begin to evaluate the extent to which these relatively simple experiments contribute to understanding and prediction of toxicant effects in more complex systems. The aspects of the life history patterns of cohorts of guppies that were examined include juvenile and adult growth and survival, age and size at first reproduction, clutch size or number of offspring produced at each reproduction, and intrinsic rate of increase (Kulbicki, 1980).

As juveniles, parental fish receiving a high ration (HR) grew significantly faster than parental fish receiving a low ration (LR). At each ration level, F-1 fish exposed to both concentrations of dieldrin grew significantly less than control fish, but there were not significant differences between growth of fish exposed to high dieldrin concentration (HD; 2 ppb in water, 4 ppm in food) and those exposed to low dieldrin concentrations (LD; 1 ppb in water, 2 ppm in food) (Figure 23).

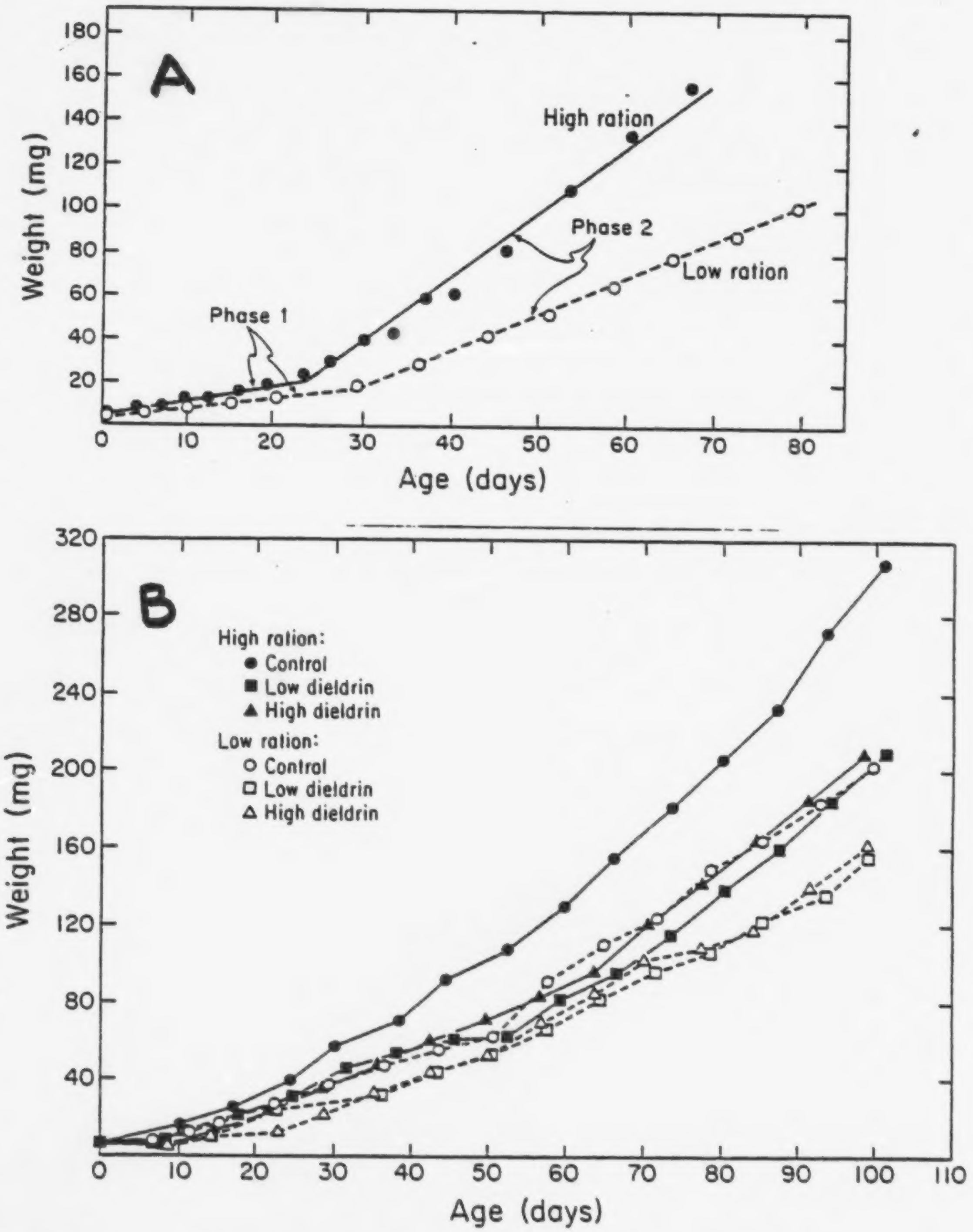


Figure 23. A. Juvenile growth of parental fish. Each point is the average of 300 fish. B. Juvenile growth of F-1 generation fish. After Kulbicki (1980).

Parental fish were first exposed to dieldrin when they reached sexual maturity. At similar dieldrin treatments, mature fish receiving the HR grew faster and attained a larger weight at each age than fish receiving the LR (Figure 24). At each ration level mature control fish had greater growth rates and attained larger weights at each age than fish exposed to dieldrin. At HR, fish exposed to HD grew more slowly than fish exposed to LD.

Cumulative juvenile mortality curves of parents and their F-1 progeny are shown in Figure 25. Some parental fish, especially at LR, were affected by disease which resulted in higher juvenile mortality of parental fish than F-1 generation control fish. In general, increased dieldrin concentration resulted in decreased juvenile survival. At LR, however, fish exposed to HD suffered less mortality than those exposed to LD. No effect of ration level or dieldrin on survival of mature fish was observed.

Age at first reproduction is an apparently important reproductive parameter, since it has a large influence on the intrinsic rate of increase, a decreasing age at first reproduction tending to increase r. Ration level had no apparent effect on age at first reproduction (Table 3). At HD, fish receiving HR first reproduced at a somewhat younger age than control fish while fish receiving LR reproduced at an older age than controls.

During their juvenile stage, fish at HR grew faster and attained a larger weight at first reproduction than fish receiving the LR (Table 3). In addition, at high ration, there was a significant reduction in size at first reproduction as a consequence of exposure to dieldrin, while at LR a slight but nonsignificant reduction was observed.

Number of offspring produced by females is apparently related to female weight and thus to previous growth history (Figure 26). At each ration level, offspring number appeared to increase as female weight

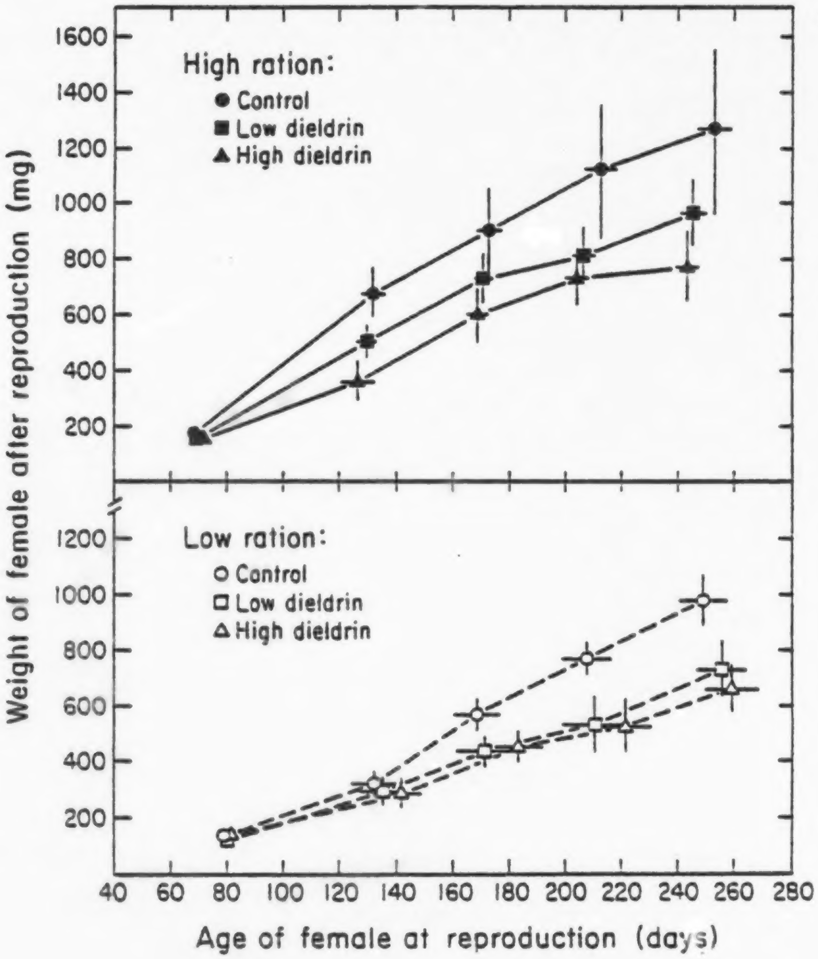


Figure 24. Effect of dieldrin on adult growth of parental fish at low and high rations. Vertical lines represent two standard deviations for female weight and horizontal lines represent two standard deviations for female age at reproduction. Each point is an average of ten fish. After Kulbicki (1980).

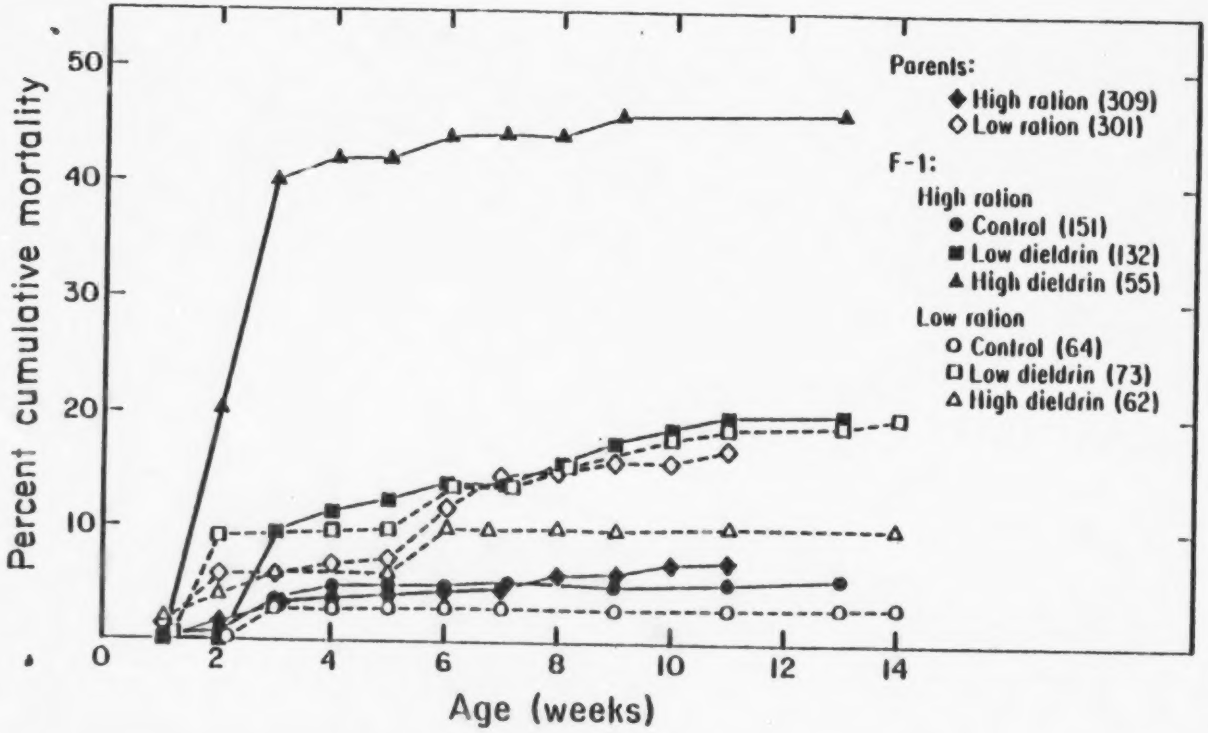


Figure 25. Cumulative juvenile mortality of parental and F-1 generation fish. The initial number of fish in each treatment is given in parentheses. After Kulbicki (1980).

Table 3. Summary of the reproductive performances of female parental fish. The first number is the mean value for ten fish and the second is $s/\sqrt{n}$. All weights are in mg.

HIGH RATION

| | Clutch number | Age (days) | Gestation period (days) | Female weight (mg) | Mean clutch size | Mean clutch weight | Mean weight of offspring |
|---|---|---|---|---|---|---|---|
| CONTROL | 1 | 131.1 | | 680 | 23.2 | 118 | 5.00 |
| | | 1.6 | | 45 | 1.7 | 14 | 0.34 |
| | 2 | 172.3 | 40.9 | 914 | 31.1 | 169 | 5.36 |
| | | 2.2 | 0.9 | 77 | 2.2 | 17 | 0.27 |
| | 3 | 212.3 | 40.0 | 1117 | 22.4 | 123 | 5.50 |
| | | 2.7 | 0.7 | 128 | 4.2 | 23 | 0.18 |
| | 4 | 252.3 | 40.0 | 1270 | 21.3 | 132 | 6.27 |
| | | 2.9 | 0.5 | 140 | 2.3 | 12 | 0.21 |

| | Clutch number | Age (days) | Gestation period (days) | Female weight (mg) | Mean clutch size | Mean clutch weight | Mean weight of offspring |
|---|---|---|---|---|---|---|---|
| LOW DIELDRIN | 1 | 129.2 | | 507 | 19.2 | 92 | 4.75 |
| | | 1.2 | | 26 | 2.1 | 12 | 0.27 |
| | 2 | 169.0 | 38.8 | 729 | 21.5 | 111 | 5.05 |
| | | 0.8 | 0.8 | 41 | 3.0 | 19 | 0.42 |
| | 3 | 207.0 | 38.0 | 816 | 34.0 | 168 | 4.96 |
| | | 1.5 | 1.0 | 39 | 4.4 | 22 | 0.17 |
| | 4 | 245.7 | 38.8 | 980 | 22.9 | 121 | 5.07 |
| | | 2.5 | 1.1 | 45 | 3.7 | 21 | 0.24 |

| | Clutch number | Age (days) | Gestation period (days) | Female weight (mg) | Mean clutch size | Mean clutch weight | Mean weight of offspring |
|---|---|---|---|---|---|---|---|
| HIGH DIELDRIN | 1 | 125.9 | | 365 | 11.9 | 48 | 4.15 |
| | | 2.3 | | 28 | 2.5 | 10 | 0.24 |
| | 2 | 168.7 | 41.2 | 600 | 11.0 | 51 | 4.22 |
| | | 1.9 | 1.2 | 41 | 2.4 | 13 | 0.30 |
| | 3 | 204.2 | 35.6 | 733 | 24.3 | 114 | 4.64 |
| | | 1.7 | 0.4 | 44 | 4.0 | 19 | 0.15 |
| | 4 | 242.3 | 37.9 | 777 | 15.9 | 83 | 5.18 |
| | | 2.1 | 0.6 | 52 | 3.4 | 19 | 0.21 |

## LOW RATION

| | Clutch number | Age (days) | Gestation period (days) | Female weight (mg) | Mean clutch size | Mean clutch weight | Mean weight of offspring |
|---|---|---|---|---|---|---|---|
| CONTROL | 1 | 132.4 | | 326 | 7.2 | 33.3 | 4.60 |
| | | 3.8 | | 22 | 1.5 | 7.0 | 0.12 |
| | 2 | 168.4 | 40.0 | 574 | 11.8 | 63.0 | 5.36 |
| | | 3.9 | 0.8 | 27 | 1.6 | 9.3 | 0.33 |
| | 3 | 208.6 | 39.6 | 779 | 14.6 | 91.8 | 6.37 |
| | | 4.0 | 0.6 | 22 | 2.0 | 12.1 | 0.25 |
| | 4 | 248.1 | 39.6 | 982 | 18.9 | 118.6 | 6.34 |
| | | 4.3 | 0.8 | 45 | 2.8 | 16.8 | 0.19 |

| | Clutch number | Age (days) | Gestation period (days) | Female weight (mg) | Mean clutch size | Mean clutch weight | Mean weight of offspring |
|---|---|---|---|---|---|---|---|
| LOW DIELDRIN | 1 | 134.1 | | 303 | 7.3 | 31.9 | 4.30 |
| | | 3.8 | | 23 | 1.8 | 7.7 | 0.14 |
| | 2 | 171.0 | 38.1 | 433 | 11.8 | 59.4 | 5.04 |
| | | 5.6 | 1.5 | 26 | 1.6 | 8.1 | 0.20 |
| | 3 | 209.4 | 38.3 | 534 | 13.9 | 72.2 | 5.17 |
| | | 5.4 | 0.9 | 46 | 2.0 | 10.9 | 0.13 |
| | 4 | 255.3 | 45.7 | 744 | 15.6 | 84.7 | 5.32 |
| | | 3.9 | 4.7 | 43 | 3.0 | 17.8 | 0.21 |

| | Clutch number | Age (days) | Gestation period (days) | Female weight (mg) | Mean clutch size | Mean clutch weight | Mean weight of offspring |
|---|---|---|---|---|---|---|---|
| HIGH DIELDRIN | 1 | 141.1 | | 306 | 4.4 | 17.6 | 3.84 |
| | | 3.4 | | 29 | 0.7 | 3.4 | 0.32 |
| | 2 | 183.0 | 42.7 | 468 | 10.9 | 54.0 | 5.01 |
| | | 4.5 | 2.4 | 29 | 1.4 | 6.4 | 0.15 |
| | 3 | 219.6 | 36.4 | 541 | 16.7 | 82.4 | 4.85 |
| | | 4.4 | 0.9 | 37 | 2.1 | 11.2 | 0.17 |
| | 4 | 258.6 | 38.9 | 673 | 10.9 | 57.0 | 5.18 |
| | | 4.2 | 1.7 | 42 | 1.9 | 10.3 | 0.18 |

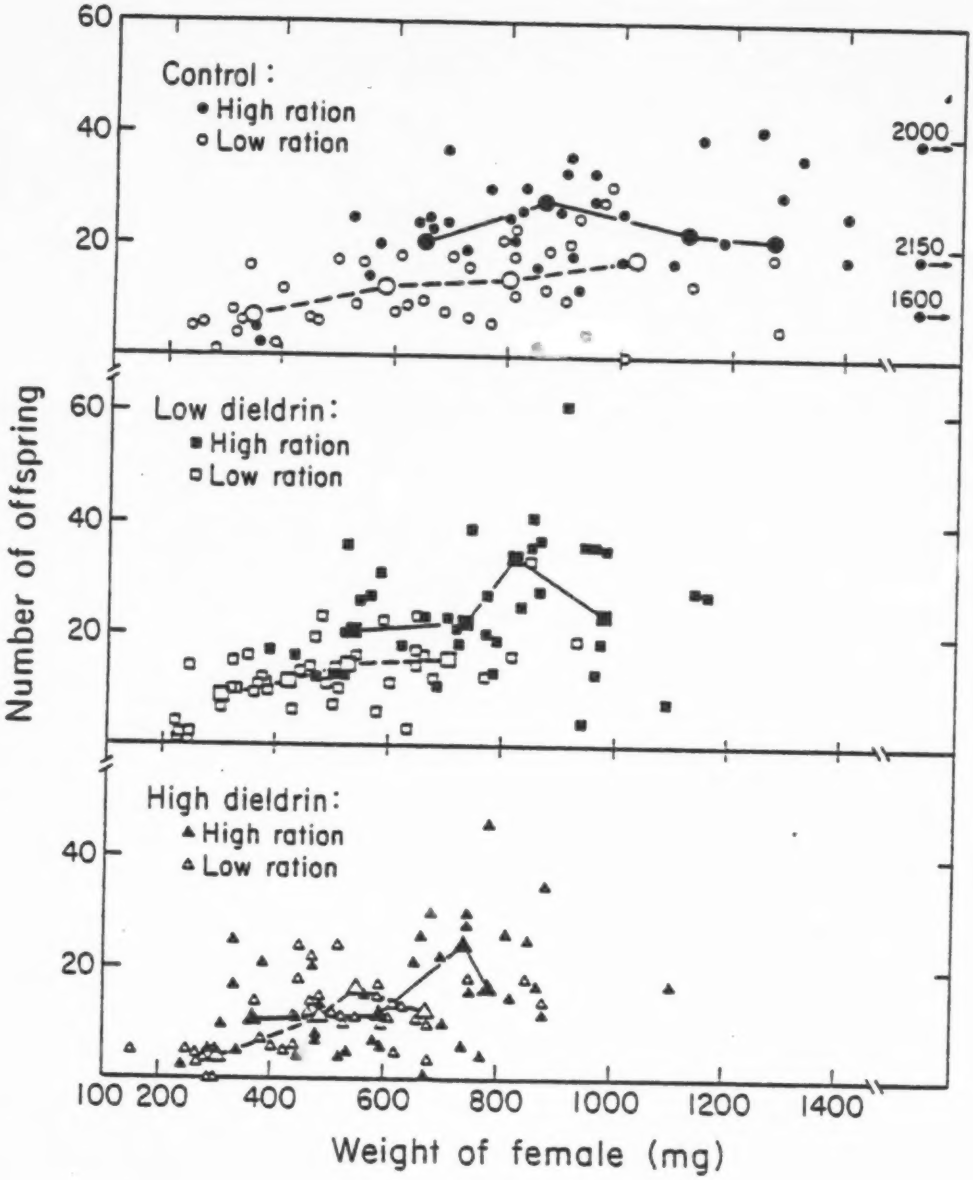


Figure 26. Relationship between clutch size and female weight. Each large point represents the average clutch size and female weight for a given gestation period. After Kulbicki (1980).

increased over a range of lower weights but, at higher weights, appeared to level off. Variability in offspring number increased with female weight.

Offspring production was dependent upon ration level as well as female weight, with fish of a given weight at LR producing few offspring than fish of the same weight at HR (Figure 26). Thus, fish of a given age at HR had larger clutches than fish of that age at LR (Table 3), both because they were larger at that age and because they ingested a greater amount of energy which could be channelled into reproductive products.

The relevance of food consumption rate and previous growth history (female weight at reproduction) to offspring production is particularly evident at first reproduction. At HR, fish were fed a greater amount of food, grew more rapidly as juveniles (Figure 23), attained a larger size at first reproduction (Table 3, and produced about three times more offspring at first reproduction than fish at LR.

Because of the apparent dependence of clutch size on female weight, there may be reproductive consequences of toxicant effects on juvenile and adult growth, with decreased growth resulting in reduction in weight of a female of a given age and consequent reduction in age-specific clutch size. But a toxicant may also directly effect clutch size, bringing about reduction in the number of offspring produced by fish of a given weight. This is evidenced by a lowering of the relationship between clutch size and body weight.

Interpretation of the effects of dieldrin on clutch size is somewhat difficult because of the relatively high variability in clutch size of fish of a given weight (Figure 26) or age, and because there was statistically significant interaction between ration level, dieldrin concentration, and gestation times, this precluded statistical comparisons (Kulbicki, 1980).

At both HR and LR, HD reduced the size of the first clutch produced by female guppies. First clutches were smaller in fish exposed to HD at least in part because their weight at first reproduction was lower than the weight of control fish. However, at low ration, size of the first clutch at HD was 40 percent lower than first clutch size at LD, even though the females maintained similar weights (303 mg at LD and 306 mg at HD). This suggests that HD may have directly affected size of the first clutch.

At HR, HD reduced both age- and size-specific clutch size for the second through fourth clutches (Table 1, Figure 26). At all dieldrin treatments at LR and LD at HR, very little effect was apparent on age- or size-specific clutch size. Even though dieldrin reduced growth and thus female weight at a given age at both LR and HR (Figure 24), by the time fish produced their second clutch they had apparently reached the plateau of offspring production for that ration so that increases or decreases in female weight at reproduction did not affect clutch size. Thus, reproductive consequences of effects on growth are mainly evident at first reproduction, over the weight range that clutch size is dependent upon body weight.

Fish receiving the HR had a greater intrinsic rate of increase (r) than fish receiving the LR (Figure 27). These differences in r can be attributed to development of different life history patterns at LR and HR. At HR, fish had greater juvenile growth, attained a larger size at first reproduction and produced a larger first clutch than fish at LR. In general, the first reproduction makes the greatest contribution to the value of r. In addition, fish at HR grew faster as adults, attained a larger size at each reproduction, and produced larger clutches at each size and age than fish at LR.

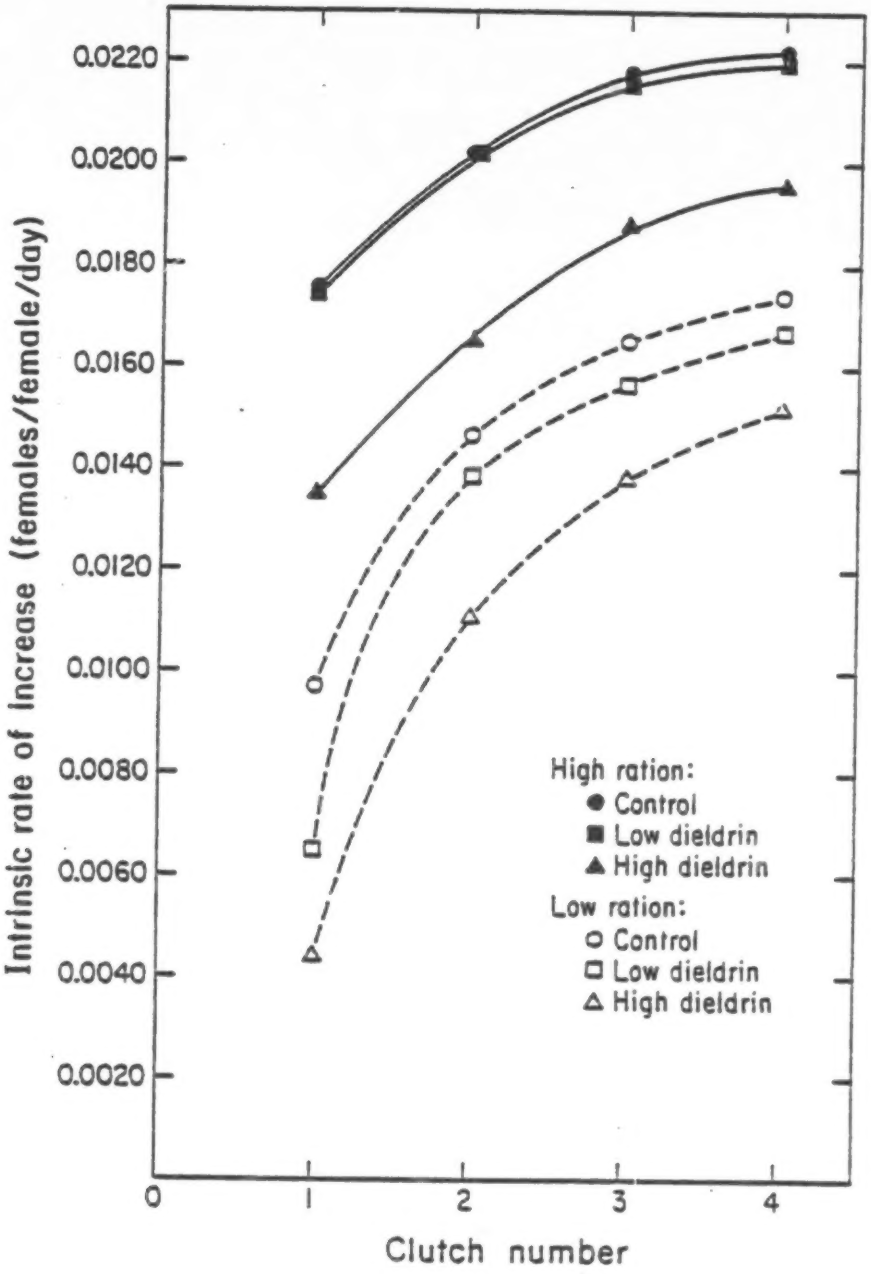


Figure 27. Values of the intrinsic rate of increase calculated for successive reproductions. Comparisons between treatments were based on the values of r at the fourth clutch. If survival and reproduction had been monitored through more than four clutches, the calculated values of r would not have been substantially different than the value r calculated at the fourth clutch (Kulbicki, 1980). Reproduction by the youngest age classes makes the greatest contribution to the value of the intrinsic rate of increase. After Kulbicki (1980).

At both ration levels, the magnitude of r for control fish and fish exposed to LD were similar. Even though fish at LD grew more slowly than control fish, there was little difference in age at first reproduction and clutch sizes between these treatments.

At both ration levels, the values of r for fish exposed to HD were lower than those of control fish. HD reduced juvenile and adult growth and the size of the first and, at HR, of subsequent clutches. In addition, at LR, HD delayed age at first reproduction.

At least at HD, dieldrin altered guppy life history patterns in relatively simple aquarium experiments in a way broadly similar to the way the toxicant altered life history patternns in the laboratory ecosystems. In the aquarium experiments and in the laboratory ecosystems, dieldrin reduced newborn survival (Figure 25), growth (Figures 16, 23, and 24), and reproduction (Figures 19 and 26; Table 3). Further possible relationships will be considered in the discussion.

## DISCUSSION

Generalizations pertaining to the organization, development, persistence, productivity and adaptation of ecological systems were presented in the introduction and will be incorporated here to account in part for the performances of the laboratory communities, thus demonstrating the usefulness and conformity with observation of such systems of generalizations. Any performance of an organismic system can be understood as the consequence of the system's capacity and of its environment. The 16 laboratory ecosystems were established with similar potential capacities for development, structure, and persistence. Their potential capacities arise from incorporation of the potential capacities of the introduced species and entail all possibilities for interactive performances of these species. Some understanding of these capacities was obtained by exposing the systems to different developmental environments, which consisted of different exploitation rates, different levels of habitat availability and energy input, and exposure to a toxicant. Under each set of environmental conditions, the systems developed steady-state structures. Thus, ecological systems can be thought of as being multisteady-state systems, with steady-state structures being determined by system potential capacity and system developmental environment. The responses of the systems to toxicant introduction was affected by conditions in the systems' environments, including rate of exploitation and level of habitat availability and energy input. At the low level of habitat availability and energy input, responses ranged from slight perturbation and subsequent recovery of system structure at zero exploitation rate to major perturbation of system structure including population extinction at 40 percent exploitation rate.

The capacities of systems are determined by the way they are organized. The trophic organization of the laboratory ecosystems entails incorporation and concordance of the capacities of the species populations. System organization underlies and determines system structure -- species kinds and densities -- under each set of system environmental conditions.

Predation, competition, commensalism, and mutualism represent classes of relationships between species populations that may be concordant. Guppies and snails are the dominant species in the laboratory ecosystems and together with amphipods appear to compete for the common food resource, organic sediments. In addition to being competitors, amphipods are also prey of the guppies. Coexistence of the competing species is not maintained simply by exploitation of one of the competitors (Paine, 1966; Menge, 1975) because all populations are able to persist at near steady-states when the guppy population is unexploited. Changes in exploitation rate, however, alter the densities of guppy populations and so indirectly affect amphipod and snail populations, this leading to different community structures (Figures 5, 7-11).

Behavior observations suggest that resource partitioning may be important in system organization and determination of steady-state structure. Guppies, amphipods, and snails feed heavily on the organic sediment derived from the alfalfa ration. But these populations also prey upon food resources other than the organic sediment. Snails appear to prey extensively upon attached algae, thus reducing overlap in food utilization between competitors. The structure and organizaton of the algal subcommunity and its role in the laboratory ecosystems, including its utilization by snails, has begun to be evaluated. Guppy populations also apparently prey somewhat upon nematodes (Finger, 1980) and perhaps other microinvertebrates as well as amphipods.

In addition, guppies may prey most extensively on the alfalfa ration just after it is introduced as it sinks through the water column and comes to rest on the surface of the rock substrate. Food material that settles into the rock substrate is not as available to the fish and is preyed upon primarily by benthic dwelling snails, amphipods, and microorganisms. Thus, partitioning of the habitat between benthic snails and amphipods and the more pelagic guppies may result in partitioning of the alfalfa food resource.

Amphipod populations maintain relatively small populations at both high and low levels of habitat availability and energy input. This results in part because of the interrelationships between the amphipod, guppy, and snail populations, with amphipods not only competing with guppies and snails for food but also being preyed upon by guppies. In addition, the food and perhaps physical and chemical aspects of the habitat may not be very favorable for amphipods. The rock substrate serves as a refugium for amphipods where they can escape guppy predation. In the presence of guppies, amphipods prefer the rock substrate, but in their absence (such as after guppy population extinction), the amphipods move freely throughout the tank. Such habitat partitioning favors persistence and coexistence of the predator and prey.

Increased habitat availability and energy input altered system structure by increasing densities of organic sediments, guppies, amphipods, and snails at each exploitation rate. On phase planes representing the interactions between populations, the relationships between population densities generated by changing exploitation rate were shifted upward and to the right (Figures 9,10,11). The structure of the microinvertebrate subcommunity was also altered with species dominance shifting from nematodes, protozoans, and ciliates at low productivity to euglenoid flagellates at high productivity (Finger 1980).

A generalized isocline model representing some possible effects on steady-state system structure and organization of energy input, exploitation, competition, presence of alternative prey, and a toxicant is shown in Figure 28. It demonstrates how population interactions including predation and competition, exploitation, and rate of energy input jointly determine community structure and organization and response to toxic substances. At each energy input rate, a relationship between predator and prey biomass defined by a prey isocline or family of prey isoclines is (experimentally or theoretically) generated by changing exploitation rate. In the generalized model, this relationship is shown to be similar to the relationship between guppy and amphipod populations at low habitat and energy input (Figure 7) or that between guppy and sediment at high habitat and energy input (Figure 11), with increasing exploitation rate bringing about reduction in steady-state predator biomass and increased prey biomass. Increased energy input rate shifts to the right on each phase plane the relationship between predator and prey biomass defined by a prey isocline or family of prey isoclines, this increasing both predator and prey biomass at each exploitation rate. Similar responses to increased energy input rate were observed in the laboratory ecosystems (Figures 9, 10, 11).

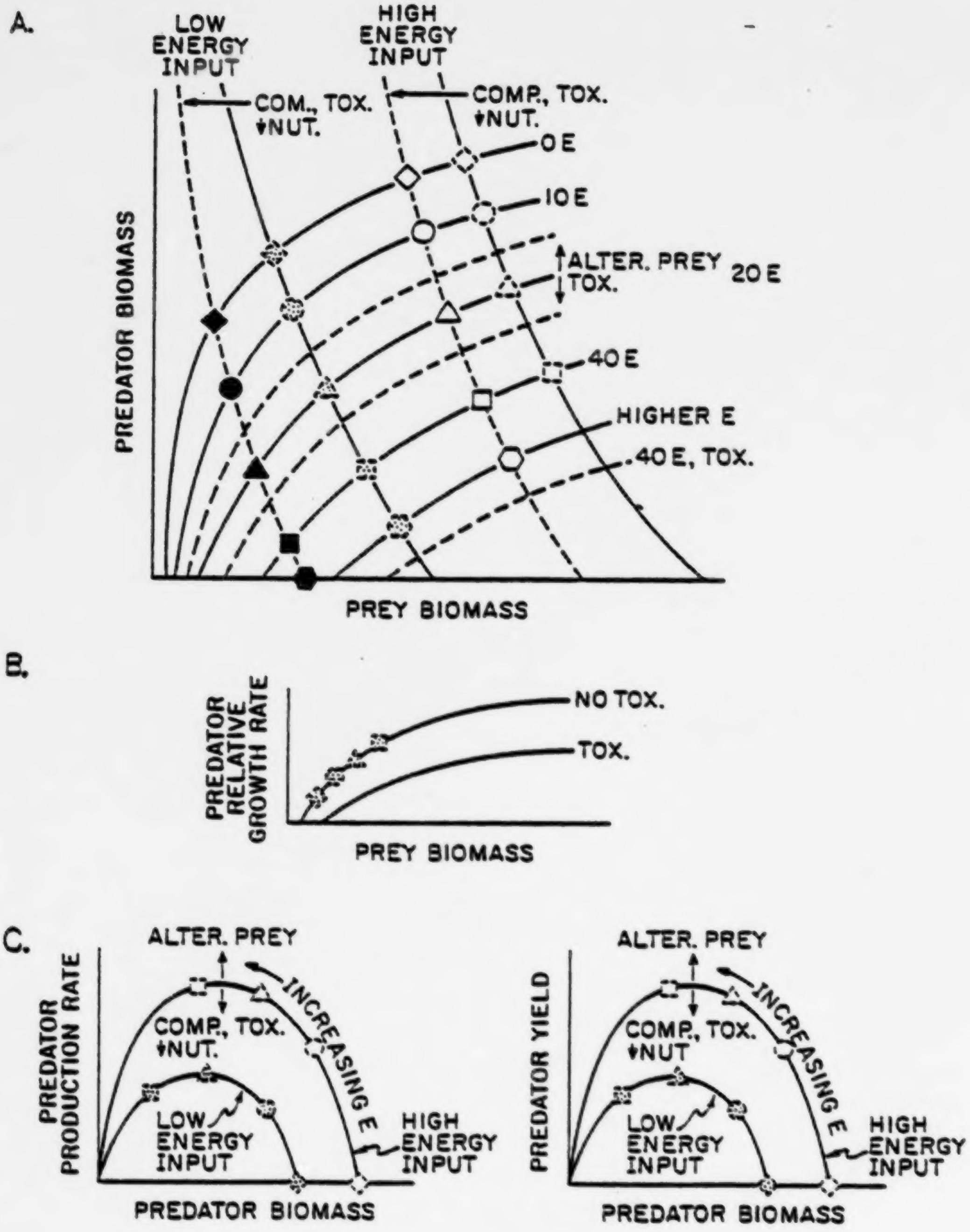
The presence of a competitor of the predator, or competitors of the prey, or competitors on lower trophic levels leading to the prey shifts to the left the relationship between predator and prey defined by the prey isoclines at each rate of energy input, resulting in reduced predator and prey biomass at each exploitation rate (Booty, 1976). Coexistence of the competitors is dependent upon rate of energy input and rate of exploitation. At low energy input, the exploited predator is capable of persisting at

Figure 28. A. Generalized phase plane and isocline systems representing the interaction between predator and prey, and some possible effects of energy input rate, competition (comp.), toxic substances (tox.), plant nutrients (nut.), exploitation (E), and alternative prey (alter. prey). Steady-state points are indicated at the intersections of predator and prey isoclines. At each rate of energy input, presence of a competitor, toxic substances, or decrease in plant nutrients can shift the prey isocline to the left on the phase plane and can cause reduction in steady-state predator and prey biomass at each exploitation rate. At each exploitation rate, presence of alternative prey can increase and toxic substances lower a predator isocline, as shown at 20E. If a predator isocline identified by a particular level of environmental factor (e.g. higher E or 40E, TOX.) does not intersect a prey isocline identified by another environmental factor or factors (e.g. low energy input with competitor present -- dashed prey isocline), then the predator population cannot persist under that set of environmental conditions (solid hexagon).

B. Theoretical relationship between predator relative growth rate and prey biomass showing direct effect of a toxicant on growth rate relationship.

C. Predator steady-state production and yield curves and how the magnitudes of these curves can be affected by energy input, competition, toxicants, plant nutrients, and alternative prey. Each curve is derived from a prey isocline on the predator-prey phase plane.

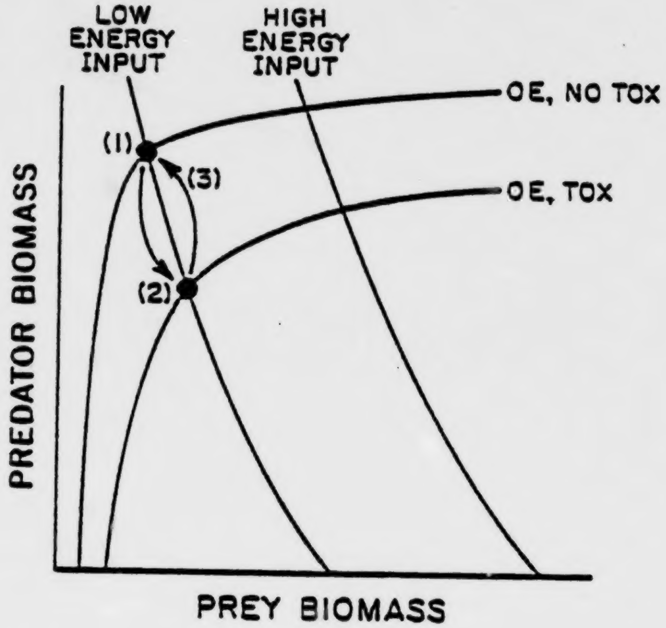
Figure 28.

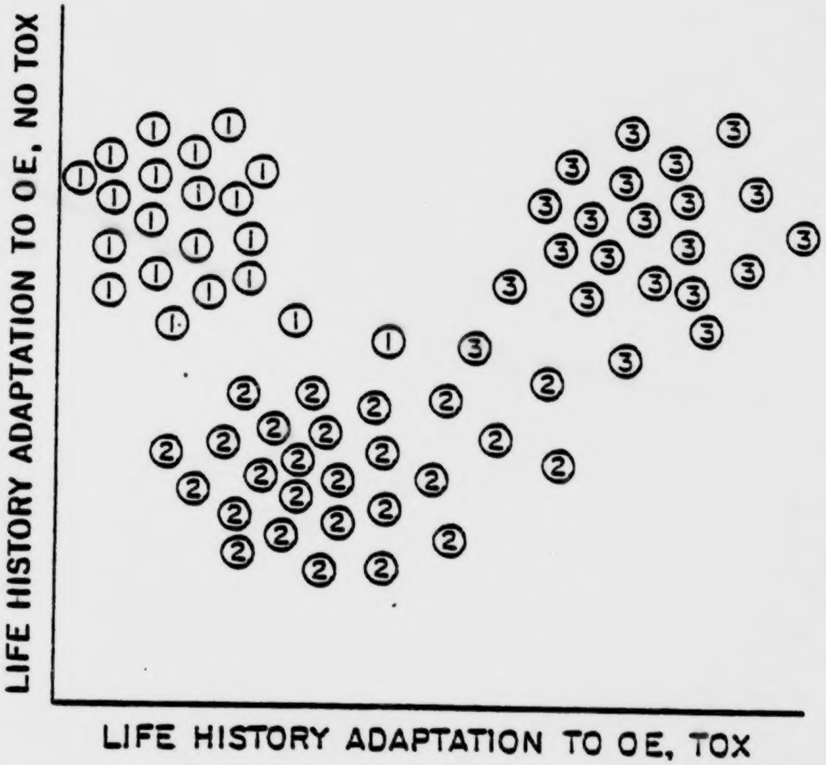

A.
LOW ENERGY INPUT
HIGH ENERGY INPUT
COM., TOX. ↓NUT.
COMP., TOX. ↓NUT.
0 E
10 E
↑ALTER. PREY ↓TOX.
20 E
40 E
HIGHER E
40 E, TOX.
PREDATOR BIOMASS
PREY BIOMASS
B.
PREDATOR RELATIVE GROWTH RATE
NO TOX.
TOX.
PREY BIOMASS
C.
ALTER. PREY
COMP., TOX. ↓NUT.
INCREASING E
LOW ENERGY INPUT
HIGH ENERGY INPUT
PREDATOR PRODUCTION RATE
PREDATOR BIOMASS
ALTER. PREY
COMP., TOX. ↓NUT
INCREASING E
LOW ENERGY INPUT
HIGH ENERGY INPUT
PREDATOR YIELD
PREDATOR BIOMASS

high exploitation rates (higher E) in the absence of competiton (dotted hexagon). But, in the presence of the competitor, the predator isocline identified by "higher E" does not intersect the prey isocline (dashed isocline). Coexistence is not possible under these conditions and the heavily exploited predator is driven to extinction (solid hexagon). The exploited predator and its competitor are capable of coexisting at lower exploitation rates (other solid symbols), or at high exploitation rates (higher E) at the high rate of energy input (open hexagon). The presence of additional or alternative prey for the exploited predator shifts the predator isocline upward at each exploitation rate and thus may facilitate coexistence of competitors at the low level of energy input. Exploitation or predation on the competitor (cf. Paine, 1966; Menge, 1975) would tend to reduce the amount of leftward shift of the prey isocline and thus would also facilitate coexistence at high exploitation rates.

A competition phase plane relating the biomass of the exploited predator to the biomass of its competition can also be constructed. Like the predator-prey phase plane shown in Figure 29, the competition phase plane could illustrate the effects of exploitation, predation, energy input, and other environmental conditions on steady-state bomasses of the competing populations (Booty, 1976; Liss, 1977). Relationships similar to those between guppies and snails (Figures 8 and 10) could be deduced. Increases in exploitation rate could be shown to bring about reductions in the density of the exploited predator (the guppy) and increases in the density of the competitor (the snail), with the relatonship between the competitors being shifted to the right on the competition phase plane with increases in energy input rate. Thus, in Figure 29, at each energy input rate, the presence of a competitor shifts the prey isocline to the left

Figure 29. Possible changes in steady-state predator population adaptive capacities corresponding to changes in steady-state predator population densities. Each circle represents how well an individual is adapted to each of two sets of environmental conditions, OE, No Tox and OE, Tox. The set of circles labelled with (1) represents the adaptive capacity of the population when it is at steady-state at low energy input, OE, No Tox. The individuals are not well adapted to toxicant. Introduction of toxicant reduces steady-state predator population density (2). But the population adapts evolutionarily to the toxicant and increases in density (3). It is now reasonably well adapted to toxicant and has evolved a different capacity at (3) than it had at (1).


LOW ENERGY INPUT
HIGH ENERGY INPUT
OE, NO TOX
OE, TOX
(1)
(3)
(2)
PREDATOR BIOMASS
PREY BIOMASS


LIFE HISTORY ADAPTATION TO OE, NO TOX
①
②
③
LIFE HISTORY ADAPTATION TO OE, TOX

and steady-state competitor biomass increases as the biomass of the predator is reduced by exploitation.

The presence of a toxic substance can have diverse and complex effects on community structure and organization, some of these possible effects being illustrated in Figure 28. If a toxicant directly affected the prey or affected lower trophic levels leading to the prey, the relationship between predator and prey defined by the prey isocline would be shifted to the left at each energy input, reducing predator and prey biomass at each exploitation rate. Inhibition by toxicants of the activities of decomposers may lead to reduction in rate of regeneration of plant nutrients (N) and will likely alter the position of prey isoclines. Such leftward shifts in prey isoclines, may jeopardize predator persistence at higher exploitation rates and lower energy input rates.

A toxicant directly affecting predator survival, growth, or reproduction can shift the predator isocline downward at each exploitation rate, bringing about reduction in predator biomass. Such an effect on predator relative growth rate is shown in Figure 28B. As a result of the downward shift in predator isoclines, heavily exploited predator populations in systems with low rates of energy input may be the most vulnerable to extinction as a result of exposure to toxicants.

In the laboratory ecosystems, dieldrin directly influenced only the guppy populations, in effect lowering the predator isoclines at each exploitation rate and thus bringing about reduction in the biomasses of populations exploited at 0.10, and 20 percent and apparently causing extinction of the population exploited at 40 percent (Figure 12). Since an increase in input rate of energy and materials shifts the prey isocline(s) to the right, populations exploited at 40 percent at the high level of habitat and availability and energy input may be capable of persisting when exposed to 1 ppb of dieldrin. The effect of increased energy input rate on the response of the laboratory communities to dieldrin is presently being evaluated.

Toxicant effects on populations, including extinction, are not a simple consequence only of conditions in the environment of the community such as exploitation and energy input, but are determined also by the organization of the community. The presence of competitors of guppies for the organic sediment food resource (snails, amphipods) in effect, shifted prey isoclines to the left at each energy input rate and by so doing may have facilitated guppy population extinction. This is to say that had competitors of the guppy not been present, they may have been able to persist at higher exploitation rates in the presence of dieldrin.

Changes in population abundance can be operationally accounted for in terms of rates of gain and loss of population biomass and how these rates are affected by environmental conditions. Population production and yield are rate terms that have been of special interest to biologists. Each particular production and yield value is a consequence of the population's capacity for production and yield and conditions in the population's environment, in a way that changing environmental conditions bring about changes in the production and yield of a population with a given capacity.

Communities provide the environmental context for populations. Thus, the organization of the community of which a population is a part as well as factors such as energy input rate and exploitation rate fundamentally influence the abundance, production, and yield of a population of interest. Ivlev (1945) recognized the importance of ecosystem organization in determining population production. He distinguished production on the particular density-dependent rate of tissue elaboration of a population of interest from the productivity of an ecosystem, on its ability to support population production. This view of ecosystem productivity has been extended and has proven useful in explanation and understanding of salmonid production in laboratory streams and how it is affected by various pollutants (Brocksen, Davis, and Warren, 1968, 1970; Warren, 1971). Using isocline theory, Booty (1976) formalized productivity theory. Liss (1977) articulated fisheries exploitation theory with productivity theory by dealing with the ability of ecosystems to support population recruitment and yield as well as production.

Predator production and yield bear dome-shaped relationships to predator population biomass. Predator production can be computed as the product of predator relative growth rate and predator biomass. Each steady-state predator production curve is derived from a prey isocline defining a density-dependent relationship between steady-state predator and prey biomass, and from a relationship between steady-state predator relative growth rate and prey biomass as shown in Figure 28. Each production curve is taken to define a level of ecosystem productivity, including all production values associated with different biomasses along it. Each yield curve is also derived from a particular prey isocline (Liss, 1977).

Any change in the position or form of either the relationship between steady-state predator and prey biomass defined by a prey isocline or in the relationship between predator growth rate and prey biomass will lead to a change in the magnitude and form of the steady-state production and yield curves, this defining a change in system productivity.

Increased ecosystem productivity can result from increased rate of energy input, which shifts the prey isocline to right on the phase plane and increases the magnitude of the production and yield curves. Changes in exploitation rate, however, alter neither the position of the prey isoclines or the predator growth rate relationship and thus do not constitute changes in productivity, according to the isocline system. Increased exploitation rate results in decreased predator biomass and increased prey biomass, shifting the steady-state point downward along a particular prey isocline and to the left, toward the origin, on the curves of production and yield.

In the laboratory ecosystems, increased habitat availability and energy input shifted the relationships between guppy biomass and the biomass of their prey to right on phase planes (Figures 9,10,11) and increased the magnitude of guppy production and yield curves (Figure 14). Changes in guppy exploitation rate did not appear to alter the magnitude of the curves, but rather shifted guppy biomass along each of the curves.

The presence of competitors of the predator or competition on lower trophic levels leading to the predator shift the prey isoclines to the left and thus lead to decreases in system productivity and reductions in the magnitude of predator production and yield. Reduction rate of regeneration of plant nutrients has a similar effect. Exploitation of the predator population can alter system productivity by removing materials from the system that would otherwise have decomposed to plant nutrients. The presence of additional prey, so long as they are not competitors, can increase system productivity by effectively increasing predator growth rate relationships (Liss, 1977).

Toxic substances can alter the productivity of an ecosystem for a population of interest by causing shifts in the position of the prey isoclines or by altering the predator growth rate-prey relationship (Figure 28). If a toxicant adversely affected the prey or lower trophic levels leading to the prey (plants, etc.), the prey isocline could be shifted to the left on the phase plane and the magnitudes of predator production and yield could be reduced. A toxicant could, however, increase predator abundance and increase the ability of the system to support predator production and yield if it selectively reduced the abundance of the competitor, this effectively shifting prey isoclines to the right on the phase plane.

A toxicant directly altering the relationship between predator growth rate and prey biomass can result in reduction in system productivity and decrease in the magnitude of predator production and yield curves (Figure 28C). In the laboratory ecosystems this appears to be the mechanism by which guppy production and yield curves were lowered. Dieldrin directly affected guppy populations, apparently by reducing not only guppy relative growth rate (in effect the relationship between growth rate and prey biomass) but also guppy reproduction and survival. Evaluation in separate aquarium experiments of the effects of dieldrin on prey and competitors of guppies indicated that these organisms would probably not be affected by 1 ppb of dieldrin introduced into the laboratory ecosystems. Thus, any changes in their abundance probably resulted from changes in guppy population biomass induced by dieldrin.

Populations come to have their capacities to persist and their capacities for production and yield through incorporation of the life history capacities of their individuals. But how are the life history capacities of individual organisms related to population density and community structure? Many kinds of toxicity tests are intended to evaluate toxicant effects on aspects of individual organism life histories, including survival, growth, and reproduction. Undertanding the relevance of results of these tests must be based upon some understanding of the relationhip between life histories and community structure.

Individual organisms have capacities to alter their life history patterns in response to changes in their environments and in ways favoring the persistence of their populations under these conditions. Through such developmental as well as evolutionary alterations in life history patterns, individuals and their populations maintain concordance with their environmental systems. The community provides the environmental context in which individuals develop and populations must be adapted to persist. Different community structures -- different kinds and densities of prey, predators, and competitors -- constitute different developmental environments forindividuals and different evolutionary environments for populations. Changes in community structure bring about changes in the kinds of individual organism life history capacities composing populations and changes in individual organism life history patterns. Thus, different life history patterns can be associated with different community structures.

In the laboratory ecosystems, changes in conditions in the environment of the community such as exploitation rate, habitat availability and energy input, and exposure to toxic substances alter steady-state community structure. Different steady-state guppy life history patterns existed at different community structures. This may be best illustrated by referring to the generalized model shown in Figure 28. At each level of energy input, increases in exploitaton rate result in reduction in steady-state predator biomass and increases in steady-state prey biomass. Steady-state predator life history patterns that may exist at lower and higher exploitaton rates are summarized in Table 4.

As exploitation rate and, thus, mortality due to fishing increase, we might expect reduction in length of life and number of clutches produced in an individual's lifetime. But due to reduction in predator biomass and increase in the biomass of their food resource, we might also expect faster

Table 4. Some possible predator life history patterns at low and high exploitation rates (After Kulbicki, 1979).

| Life History Traits | Low Exploitation Rate | High Exploitation Rate |
|---|---|---|
| Longevity | long lifespan<br>low adult mortality | shorter lifespan due to very high mortality resulting from exploitation. |
| Number of clutches in a lifetime | many due to long lifespan | fewer due to the high mortality and shorter lifespan |
| Growth Rate | low due to low food availability and high population density | high due to high food availability and low population density |
| Age at first reproduction | later due to low food availability and low adult mortality | earlier due to high food availability and/or higher mortality |
| Size at first reproduction | smaller due to slower growth | larger size at first reproduction |
| Clutch size | low food availability will result in small clutches | larger clutches because of high food availability and better growth |

juvenile and adult growth (Figure 16), increased size at first reproduction (or perhaps decreased age at first reproduction), and increased fecundity (Figures 17 and 19). Thus, when guppy populations are exploited at high rates, they may develop life history patterns normally associated with higher values of the intrinsic rate of increase - more rapid growth, earlier maturity or larger size at maturity, and higher fedundity at first and at subsequent reproductions. Such life history characteristics can be understood as adaptations to environments that bring about shortening of lifespan and reduction in number of clutches in a lifetime. That populations come to be composed of individuals that have life history capacities to exhibit these kinds of life history characteristics enables the populations to persist at high exploitation rates. Populations whose organisms cannot manifest these kinds of characteristics may not be able to persist at high levels of exploitation.

These kinds of changes in life history pattern in response to exploitation are familiar to fishery biologists. They have been observed in the laboratory ecosystems and in other exploited guppy populations (Liss, 1974), in clupeids (Burd and Cushing, 1962; Beverton, 1963), in trout and perch (Alm, 1959), and in whitefish (Miller, 1956). This suggests that these kinds of changes in life history patterns may be important, but they are not the only ways that populations adapt to high exploitation rates.

Murphy [redacted] (1967,1968) believed that sardine populations adapted with long life and many reproductions to life in highly variable oceanic environments where probability of successful reproduction in any one year is very low. Heavy exploitation of the California sardine reduced sardine lifespan and thus the number of possible times a sardine could reproduce in its lifetime, essentially stripping away the mechanism that had adapted the sardine to life in highly variable environments. Severe reductions in the sardine population took place and a most valuable fishery collapsed.

Toxic substances can have similar kinds of effects on adaptive capacities, altering life history patterns so that populations are no longer able to persist or may persist at reduced densities under given sets of environmental conditions. In the laboratory ecosystem, dieldrin apparently altered guppy life history patterns by reducing growth and fecundity and, at 40 percent exploitation, by increasing mortality of offspring. At the 40 percent exploitation rate, dieldrin may have caused extinction of the population by effectively preventing the individuals from exhibiting the life history patterns -- more rapid growth, higher fecundity, increased offspring survival -- that adapted the population to persist at this very high exploitation rate. These changes in life history pattern effectively lower the predator isocline at 40 E, as shown in Figure 28, until it does not intersect the prey isocline.

Such heavily exploited populations, where rapid growth, high fecundity, and good juvenile survival are essential for persistence, may be more "sensitive" to reductions in growth, fecundity, and survival caused by toxic substances. At lower exploitation rates, alterations in life history pattern caused by dieldrin resulted in reductions in guppy population density, but the populations were able to persist. But surely higher concentrations of toxicant, which would bring about more severe alterations in life history patterns -- greater reductions in growth, fecundity, and survival -- would cause extinction of populations exploited at lower rates.

Now, at the higher rates of energy input, because of the greater availability of food, a population may be able to persist when exposed to a toxicant and exploited at 40E, as shown in Figure 28. The range of exploitation rates over which populations can persist when exposed to a given level of toxicant may be greater at high energy input rates than at low rates. But there will surely be some exploitation rate higher than 40E at which the population at a high energy input rate will not be able to persist.

Exploitation and exposure to toxicants alter adaptive capacities of populations by bringing about evolutionary changes in the kinds of individual organism life history capacities composing the populations. The guppy population, exploited at 0 percent in the laboratory ecosystems, probably underwent evolutionary changes in becoming more "resistant" to dieldrin and recovering from perturbation.

Evolutionary alteration in adaptive capacity can be illustrated with graphs resembling Levin's (1968) fitness sets. Each point in Figure 29 represents the life history capacity of an individual organism. Its position indicates how well the life history pattern exhibited by the individual under each set of environmental conditions is adapted to those conditions. The set of all individual organism life history capacities defines the steady-state adaptive capacity of the population at OE, No Toxicant (1) OE, Toxicant (2); OE, Toxicant After Recovery (3). Exposure to toxicants altered adaptive capacity, with the composition of the population shifting from one in which most individuals were poorly adapted to OE, Toxicant (1) to one in which most individuals are well-adapted to these conditions (3). Thus, even though the population while being exposed to the toxicant, has returned to the density it maintained prior to toxicant introduction, it has a very different capacity. It has adapted evolutionarily to the toxicant. But, in adapting to the toxicant, the population may have lost its adaptive capacity for other environmental conditions.

In the laboratory ecosystems, populations exploited at 10 and 20 percent did not recover from toxicant perturbation throughout the time that dieldrin was being introduced. The unexploited population maintained a greater density than the populations exploited at 10 and 20 percent. Perhaps greater population density increased the probability that "resistant" individuals were present in the population and so speeded evolutionary adaptation and recovery from perturbation.

Populations adapt to changes in conditions in their environment through life history and evolutionary adaptation. Toxic substances can alter individual organism life history patterns and the adaptive capacities of populations and thus bring about changes in population densities and community structure. Many kinds of toxicity tests are intended to provide evaluation of hazards of toxic substances based upon their effects on aspects of individual organism life histories. But in order to be useful in this regard, toxicant effects observed in simple toxicity tests must bear some relation to possible effects the toxicant may have upon life histories, populations, and communities in natural ecosystems.

Aquarium experiments intended to evaluate the effects of dieldrin on guppy life history patterns were conducted in conjunction with the laboratory ecosystem studies. This provided the opportunity for examining some of the possible relationships between effects observed on life history patterns in experiments more like simple toxicity tests with effects on life history patterns, populations, and communities observed in the laboratory ecosystems. Understanding the relevance of test results on life history patterns must be based at least in part upon an understanding of the relationship between life history pattern and community structure.

We have shown how different guppy steady-state life history patterns can be associated with different steady-state comunity structures in both the laboratory ecsystems and with the generalized isocline model (Figure 30, Table 4). In particular, changes in exploitation rate brought about changes in steady-state life history pattern, population density, and community structure. Increased exploitation rate resulted in reduction in population density and density-dependent increases in size-specific growth and reproduction occasioned by increased food availability. Steady-state age- and size-specific patterns of growth and reproduction at low and at high exploitation rates (Table 3, Figures 15-19) are broadly similar to guppy life history patterns observed at LR and at HR, respectively (Figures 23-27). Thus, different food rations in aquarium experiments generated life history patterns similar to those at different exploitation rates (with the exception, of course, that exploitation reduced lifespan and number of clutches).

Using isocline and other ecological theory, perhaps such meaning and relevance can be "written onto" life history patterns observed in individual organism experiments. That is, the theory gives the results of these experiments meaning. In the broadest sense, perhaps life history patterns observed in these simple experiments can be thought of as steady-state life history patterns that would exist at some steady-state community structure generated by some fixed set of community environmental conditions.

This provides at least some rationale for evaluating toxicant effects on life history patterns under different sets of important environmental conditions, for the life history patterns that develop under these conditions may be taken to represent those that would develop at different community structures. One important environmental factor is food availability. Determination of life history patterns at different levels of food availability may at least begin to be representative of life history patterns that would develop if changes in community environmental conditions or community organization altered prey densities. These might include changes in exploitation rate (or mortality rate), changes in energy input at a given exploitation rate, or introduction of a competitor (Figure 30). It is important to realize, however, that other factors as well as alteration in prey density mould life history patterns.

In the aquarium experiments, dieldrin reduced newborn survival (Figure 25), juvenile and parental growth (Figures 23 and 24), and clutch size (Table 3, Figure 26). As far as we were able to ascertain, these same kinds of effects on guppy life history patterns occurred in the laboratory ecosystems. (Figures 16 and 19). But effects on population abundance and persistence resulting from exposure to dieldrin ranged from perturbation and recovery at zero exploitation rate to extinction at 40 percent exploitation rate. It is far less easy to see how such a diversity of effects could have been anticipated from the individual organism experiments. However, it is possible that with appropriate theory, such effects may have become more apparent. Perhaps the point here is that interpretation of individual organism experiments, if they can be given meaning at all, is not a simple matter of direct extrapolation to complex systems, but entails the use of theory as a "vehicle" for extrapolation, and it is in the context of such theory that results of relatively simple tests on individual organisms may find meaning.

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